인류학 박사 학위논문

Evolutionary Anthropological Analysis of Dysfunctional Behavioural Patterns

- Focusing on Defence Activation Disorders

역기능적 행동 패턴의 진화인류학적 분석

- 방어활성화장애를 중심으로

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Abstract

Evolutionary Anthropological Analysis of Dysfunctional Behavioural Patterns

- Focusing on Defence Activation Disorders

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Like the human body, the human mind is the product of evolution. The emotional system is also an adaptive trait created through a long evolutionary history. Psychological defence mechanisms are related not only to several emotions such as depression, anxiety, obsession and compulsion, but also to a variety of dysfunctional behaviours such as withdrawal, obedience, voluntary defeat, avoidance, helplessness, and perseveration. Excessive activation of defence modules leads to some dysfunctional outcomes, which can be broadly classified to defence activation disorders. Depressive disorder, anxiety disorder, obsessive-compulsive disorder, and other defence activation disorders harm individual well-being and lead to high mortality and low fertility. Additionally, dysfunctional disorders have high prevalence rates and high heritability. Several hypotheses have been proposed to explain the paradoxical phenomenon of low fitness, high prevalence, and high heritability, but each theory has its limitations.

In this study, the emotional system is considered as a superordinate cognitive module for grasping the average resource amount and the average diminishing returns of resources, based on the Marginal Value Theorem. Under the assumption, the quantitative behavioural currency for emotional states was proposed for estimating individual fitness. Also, it was verified that individuals utilising suboptimal strategies can be stably maintained in agent-based evolutionary simulation environments. Individuals tended to gather at the proper area for their *d-value*. Individuals were adapted to have different *d-values* according to the local niche, and their proportions have inversely correlated each other. The simulation runs stably within the calibrated range of the variables for a long time.

The mechanism of niche specialisation may keep the balanced proportion of subpopulations with suboptimal *d-value*. Agents establish locally optimal strategies based on their given *d-values*, and the relative proportion of subpopulation maintained stably in the heterogeneous habitat with the resource gradient. Also, then, possible ecological factors affecting fitness were clarified, such as the movement cost, minimal energy for reproduction and environmental heterogeneity. First, movement cost is the deterministic factor to limit the free dispersion in the habitat. As it increased, the population declined, especially subpopulation with high levels of defence. Second, the rise in minimum energy for reproduction limits population growths. Notably, highly defensive individuals are much vulnerable to increased reproductive cost. Several other simulation results and their implications are also portrayed.

Moreover, it was discussed what evolutionary hypotheses were mainly compatible with the results of the study. Balancing selection appears to be a plausible evolutionary mechanism, at least within the agent-based simulation environments, that makes the suboptimal levels of defence activation the evolutionarily stable strategies. Also, the rapid change of situations such as rising of movement cost or reproductive cost seems to have negative influences, esp., to highly defensive individuals. The mismatch hypothesis may explain why individuals with highly activated defence modules show

rapid progression of dysfunctionality after facing environmental changes.

This study is the first research to verify the ultimate causes of defence activation disorders in computer-simulated environments by using agent-based modelling with the theoretical basis of the Marginal Value Theorem. At the end of the paper, some arguments about the prospect of human behavioural researches with the agent-based modelling in the field of evolutionary anthropology are discussed.

Keywords: defence activation disorder, evolutionary psychiatry, human behavioural ecology, mental disorder, agent-based simulation

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Chapter 1. Introduction

The introduction is divided into two parts. The part I part sketchily describes the evolutionary anthropological concept, diagnostic classification, and psychiatric implications of defence activation disorders. It also briefly explains the current evolutionary hypotheses about mental disorders including defence activation disorder and summarises the pros and cons of those hypotheses.

The part II suggests the balancing selection model as one of the plausible evolutionary hypotheses explaining the cause of defence activation disorder. An intermediate model was required to clarify the relationships between defence level and the fitness. To build the intermediate model, cognitive behavioural traits of psychological defence mechanism were converted into ecological currency by the Marginal Value Theorem (MVT).

Part I

The definition and the classification of mental disorders were mostly described on the basis of clinical usefulness. Therefore, those are usually unsuitable for evolutionary researches. Part 1 illustrates a new evolutionary concept of defensive activation disorder as dysfunctional behavioural patterns, and the evolutionary paradox of them. Several hypotheses have been proposed to explain the evolutionary paradox, but none are entirely satisfactory.

1. Defence Activation Disorders and Evolutionary Paradox

Charles Darwin said that emotions such as fear are innate, highly specific to situations and the product of coordinated brain activities, and that different animal

species with diverse environmental demands (or histories) have evolved unique, specialised sets of fear (or defensive) responses to maximise survival (Darwin 1998). Sigmund Freud argued that humans use a defence mechanism to reduce anxiety arising from unconscious conflicts (Spielman 2001). However, defence mechanisms in evolutionary psychiatry refer to adaptive responses in which individuals maximise their fitness from threatening environmental stimuli toward them. In an evolutionary context, the term fitness is a quantitative representation of natural selection or sexual selection. It refers to the ability of a genotype or phenotype to survive in the environment and produce offspring. So, as behavioural strategies to avoid risk and reduce conflicts, defence mechanisms are adaptive survival and reproductive strategies (Nesse 2001).

Organisms have evolved to maximise fitness by reacting appropriately to various stimuli that occur within and outside of their bodies. Emotions are the evolutionary product of the brain's effort to regulate physiology and behaviour to gain benefits under certain conditions (Gluckman, et al. 2009). Humans tend to act according to individual goals, thus mapping these goals can help to estimate how emotions might have benefited potential fitness (Gluckman, et al. 2009). For example, in a variety of social or non-social threat situations, individuals respond in ways to protect themselves from potential or actual threats (Gilbert and Allan 1998). For example, individuals may use social avoidance, social withdrawal, arrested fight, blocked escape, or involuntary subordination as defensive behavioural strategies (Sloman and Gilbert 2000).

However, defensive behaviour is deeply related to negative emotions triggered by unfavourable ecological or social cues (Damasio 2003). Emotions with negative valence are often considered undesirable and unhealthy. Negative emotions generally pertain to the difficulties of life, such as family death, separation, isolation, unemployment, loss of status, physical illness, social trauma, and excessive stress. Therefore, depression, anxiety or disgust are often regarded merely as unwanted consequences by undesirable internal or external happenings. “Avoid it, if you can”.

However, overactive defensive behaviours could be normal responses with

adaptive value, despite their accompanying subjective uncomfortable feelings (Haselton and Buss 2000). The trade-off between costs and benefits depends not on the individual's well-being but on reproductive fitness. Even if some emotional responses are unpleasant, it could be adaptive traits if they increase the fitness of individuals or their relatives. Thus, excessive activation of some defence modules is evolutionarily inevitable (Nesse 2005).

Unpleasant emotions such as easily activated fear response, constant level of anxiety or irritating obsessive-compulsive preoccupation could make adaptive sense (Cartwright 2016). Whereas, sadness or depression weakens our motivation to continue with the additional pursuit of goals and strengthens the tendency to keep the current positions. They can conserve resources since they are unrewarding (Price, et al. 1994; Watson and Andrews 2002). On the contrary, joy or happiness works as a device to encourage specific actions and encourage new attempts (Gluckman, et al. 2009).

This concept can also be applied to behavioural responses such as fear of danger, the depressive reaction toward stress, anxiety about threats, interpersonal avoidance, and aversion to contamination. Sometimes, highly defensive behaviours could be adaptive because the potential benefits from overactive defence responses are higher than their costs (Nesse 2005). Prepared fear responses to risk factors frequently encountered in an EEA (Environment of Evolutionarily Adaptedness) (McNally and Reiss 1982), for example, fear about outgroup (Quillian and Pager 2001), anxiety about potentially sick people (Faulkner, et al. 2004), and aversion to potentially contaminated foods (Rozin and Fallon 1987) are considered ecologically relevant activations of psychological defence modules.

Therefore, defence mechanisms can cause unpleasant responses to individuals, but cannot be considered maladaptive because they have the advantage of improving fitness (Nesse 2005). Activation of defence modules inevitably leads to issues concerning false positives or false negatives. A defence module is activated in a desirable situation (false positive), and a defence module is not activated in an

undesirable situation (false negative) (Nesse 2001). According to the Error Management Theory (EMT), if the cost of false positives is less than the cost of false negatives, adaptive bias may occur to protect the individual (Haselton and Buss 2000). For example, in highly contagious environments, it would be advantageous to have a high immune response even if it causes an autoimmune or irritable immune response, rather than being susceptible to infection due to a low immune response (Williams and Nesse 1991).

However, the level of defence activation differs depending on the individual. There are many terms to refer to individual differences in behaviour, such as personality, temperament, response pattern, and behavioural syndrome. In this paper, the term behavioural pattern is used (Park 2019a). Excessive behavioural patterns are often considered unhealthy because they cause subjective discomfort and impairment of physical, mental, and social functioning. If people show excessive negative emotion or excessive defensive behaviours, they are diagnosed as clinical psychiatric disorders. In other words, they could be not only primary evolutionary adaptive responses but also maladaptive psychological responses (Park 2019a).

Dysfunctional behavioural patterns which are linked to negative emotions such as depressed mood, anxiety, fear or disgust may solve adaptive problems (Gluckman, et al. 2009). For example, specific subtypes such as postpartum depression and seasonal affective disorders are linked to particular adaptive situations. Postpartum depression plays a role in increasing resource supply from relatives in vulnerable periods after childbirth, and seasonal affective disorder plays a role in reducing unnecessary physical movements or reproductions when energy saving is needed rather than acquiring resources (Davis and Levitan 2005; Hagen 2003). According to the Diagnostic and Statistical Manual of Mental Disorders, Fifth Edition (DSM-5), these can be broadly divided into three categories: anxiety disorders, depressive disorders, and obsessive-compulsive disorders. More specifically, these include Major Depressive Disorder (MDD), Persistent Depressive Disorder (PDD or dysthymia), Generalised Anxiety Disorder (GAD), Posttraumatic Stress Disorder (PTSD), defensive Obsessive-Compulsive

Disorder (D-OCD), specific phobia, panic disorder, agoraphobia, Seasonal Affective Disorder (SAD), Avoidant Personality Disorder (APD), social phobia, and the like (Park 2019d). These are known as D-type disorders because defence behaviours are their main symptoms, although they have different clinical features, prognosis, and demographic characteristics (Del Giudice 2018).

D-type disorders, as dysfunctional behavioural patterns, can be classified into a distress cluster, which mainly shows depressive symptoms, and a fear cluster, which shows fear symptoms (Watson 2005). However, this division process is not without controversy (Table 1) (Del Giudice 2018). For example, social avoidance, which is common in social phobia, refers to feelings of discomfort of others but also accompanies fears about face-to-face interactions. The main symptoms of MDD and GAD are depressive mood and anxiety, respectively, but most of the clinical features of these disorders are often quite indistinguishable. Also, some of the obsessive-compulsive disorders do not appear to accompany internal discomfort or fear, but it is appropriate to characterise those disorders as defence activation disorders due to the pursuit of safety and revitalization of the hate system (Del Giudice 2014; Park 2019d).

Table 1 Defence Activation Disorders

Explanations		Psychiatric Diagnoses
Excessive and prolonged activation of defence modules	Distress cluster	Major Depressive Disorder (MDD), Persistent Depressive Disorder (PDD, dysthymia), Generalised Anxiety Disorder (GAD)
		Posttraumatic Stress Disorder (PTSD)
	Anxiety cluster	Defensive Obsessive-Compulsive Disorder (D-OCD)

	Specific Phobia, Panic Disorder, Agoraphobia, Seasonal Affective Disorder (SAD), Avoidant Personality Disorder (APD), Social Phobia

Conversely, if defences are excessively inactive, this can be a sign of a defence inactivation disorder (Horwitz and Wakefield 2012; Nesse 1990). Often, defence activation disorders are referred to as D-type disorders and defence inactivation disorders as d-type disorders. The DSM-5 includes the concept of defence activation disorders but does not include the idea of defence inactivation disorders because disorders are defined in terms of impairment of subjective well-being or social functioning of individuals rather than the level of evolutionary adaptation (Park 2019d). Nonetheless, excessive inactivation of defence modules may severely impair the fitness of individuals (Keller, et al. 2002). Thus, the clinical manifestations of a manic episode of bipolar disorder could be much more harmful than those of depression even though many manic patients feel happy. Manic patients who voluntarily seek medical help are sporadic compared to depressive people who tend to seek medical help voluntarily.

Excessive activation (or inactivation) of defence modules results in dysfunctional conditions within the clinical and social context. As of 2006, MDD was the seventh-ranked disease in the global disability-adjusted life years (DALYs). Excluding low-income countries where infectious and malnutritional conditions are common, the significant burden of MDD is ranked first or second in many industrialized countries (Lopez, et al. 2006).

The prevalence of defence activation disorders is quite high. The 12-months prevalence rate of MDD, PDD (dysthymia), specific phobia, social phobia, panic disorder, GAD, and OCD was approximately 7%, 2%, 7~9%, 7%, 2~3%, 2.9%, and 1.2%, respectively. The lifetime prevalence of PTSD and APD is 8.7% and 2.4%,repectively

(APA 2013).

The dysfunctional nature of defence activation disorders is not a matter of being unable to attend work or participate in social activities. Although it seems contrary to the argument mentioned above, that the overly activated defensive mechanisms have adaptive functions, defence activation disorders directly reduce the fitness of the individual. For example, the mortality rate for the population with MDD is 1.8 times higher than that of the general population. Moreover, the Total Fertility Rate (TFR) is only 0.9 compared to the general population (Uher 2009). In a variety of studies, infertility and affective disorders have been linked in a complex way, although the fertility rate of the general population varies from study to study (Williams, et al. 2007). There have been no reports of mental disorders with higher fertility or lower mortality rates. Is defence activation disorder only a physiological consequence of environmental stress, not an evolutionary trait?

However, defence activation disorder is not just psychological damage caused by environmental stress. In fact, the defence activation disorders run in families. The heritability of MDD is up to 37% (Group of the Psychiatric Genomics Consortium, et al. 2013). Twins raised in different environments also show high concordance rate. The concordance rate of identical twins reaches 46–59%, while that of fraternal twins is 20–30% (Bertelsen, et al. 1977; McGuffin, et al. 1996) when it comes to MDD. The heritability of anxiety disorders, panic disorders and social phobia ranges from 30 to 67% (Domschke and Maron 2013), 30 to 60%, and 13 to 76%, respectively (Moreno, et al. 2016).

In other words, genetic conditions that significantly lower the fitness of individuals continue at high frequencies in human populations. Although activation of defensive mechanisms contributes to the survival of individuals according to the EMT, heightened levels of defence activation seem to be related to low fitness. Despite this, defence activation still appears at a high rate in the population. It is the paradox of common, harmful, heritable mental disorders (Keller and Miller 2006).

2. Several Hypotheses for Evolutionary Paradox

Several evolutionary hypotheses have been proposed to explain this paradoxical phenomenon until now.

First, there is a hypothesis that mental disorders are common diseases. In other words, some mental disorders, including defence activation disorders, are just harmful diseases caused by accumulated mutations (Keller and Miller 2006). This explanation is hard to solve the paradox.

Second, a mismatch hypothesis or genome lag hypothesis has been proposed. The human emotional system was designed for ancient environments. In the context of modern life, the systems can appear to be suboptimal or irrational (Cartwright 2016). According to this hypothesis, defence activation disorders can occur due to the following three reasons. First, it may be a result of adaptions in past ecological conditions (ancestral adaptation hypothesis), although no improvement in fitness is currently observed (Di Rienzo and Hudson 2005). Second, in the past, the benefits and costs of fitness may not have been clear, meaning that it was a neutral trait. However, changes in the environment may have caused maladaptive consequences in modern times (Tooby and Cosmides 1990). Third, under continuous environmental changes during the Pleistocene, the fitness of defence activation disorders could have repeated periodic fluctuations, and thus may persist in the gene pool (Feinberg, et al. 2010).

However, the first hypothesis and the second hypothesis have some limitations. If defence activation disorders were desirable traits during an EEA, most people in the modern world would probably have similar traits. However, even though a significant number of people have defence activation disorders, they remain a small proportion of the total population. The second hypothesis that the benefits and costs of defence activation levels have not been evident in the past is not plausible because such psychological mechanisms have already evolved from tens of millions of years ago

(Panksepp 2004). However, the third hypothesis, that suboptimal behavioural traits persist in the population due to the periodic fluctuation of their fitness within heterogenous spatial-temporal environments, seems to provide a useful framework for understanding defence activation disorders, which will be discussed later in this paper.

Third, according to the developmental mismatch hypothesis, developmental plasticity is a useful trait for adapting to environmental changes at the individual level. It is not easy to choose and develop specific adaptive characteristics by acquiring complete information about the world during the developmental periods. So developmental plasticity leads to trade-offs that maintain uncertainty at some level (Frankenhuis and Del Giudice 2012; Frankenhuis and Panchanathan 2011). That is, genotypes with a broad norm of reaction are selected and can produce 'made-to-order' optimal phenotypes in various environments (Pigliucci and Schlichting 1998). The maladaptive learning hypothesis is also similar: specifically, individuals with a false internal working model of the world become vulnerable to numerous psychopathologies (Dimaggio, et al. 2007; Hofmann 2014; Wells 2007). This hypothesis, however, is challenging to explain dysfunctional traits that are not controlled by developmental plasticity. In addition, if individuals live in a restricted stable environment throughout their life, there should be no defence activation disorder. Also, not it does adequately explain why maladaptive learning traits have not been removed during long evolutionary history.

Fourth, according to the trade-off hypothesis, some psychological traits can be kept alive in a population group because the benefits can offset the costs. Can the Life History Theory (LHT) explain the paradox of mental disorders? However, in general, mental disorders are accompanying with high mortality and high suicide rates (Brown 1997). Despite Hagen's hypothesis that the symptoms of MDD are strategic traits for the resource request, there is no evidence that clinically depressed patients have more resources than the general population (Cartwright 2016; Hagen 2003). Moreover, since most psychological disorders occur early in life, it is tough to explain those disorders by the LHT (Andrade, et al. 2003; Bebbington and Ramana 1995; Hoek 2006; Kessler, et

al. 2005; Rutter 2005). As noted above, most mental disorders have low the Total Fertility Rate (TFR) (Baron, et al. 1982; Hennah, et al. 2003; King 2003; Williams, et al. 2007). LHT does not offer good enough evolutionary explanation of defensive activation disorder.

Fifth, according to the by-product hypothesis, individual traits governed by multiple genes have a normal distribution of variance, and thus, the extreme phenotypic variations could be diagnosed as mental disorders (Burns 2006). In other words, defence activation disorders could be by-products of the evolution of other beneficial cognitive and social traits. Generally, appropriate level of defence can enhance fitness and lead to survival benefits overall, even if unfavourable to individual well-being. However, the proportion of defence activation disorder is too high to be by-products as mentioned above. In other words, it is challenging to explain why the wide variance of the phenotype has been maintained over a long time. If natural selection worked, traits that do not produce any unfavourable by-products would be selected, and extreme end of phenotypes should be removed gradually over time.

Sixth, the cliff-edge model is a modified model of the by-product hypothesis. The cliff-edge model focuses on a highly developed central nervous system (Randall 1983; Randall 1998) or the extreme form of the psychological module (Horrobin 1996; Horrobin 1998; Horrobin 1999). Because human brain is so sophisticated and highly full of twists and turns, it could often fail seriously. In other words, mental illnesses are the results of the evolutionary path dependence. For example, the language module or Theory of Mind Module (ToMM), which are fully developed in the late teens, could be the leading causes of psychopathologies (Saugstad 1999). However, this hypothesis cannot explain the high prevalence of dysfunctional disorders and why such conditions persist. The explanation that the brain is easy to crash, because it is a highly complex organ, can be a funny analogy, but it is not a logical explanation.

Seventh, according to the inclusive fitness hypothesis, dysfunctional behavioural traits can be continued through kin selection. This hypothesis is a trade-off hypothesis

at the kin level. For example, even suicidal behaviour can be sustained by natural selection hypothetically if it can offer enough benefits to genetic families (De Catanzaro 1991). Some studies suggest that self-perceptions such as 'I am a burden to my family' under the situation of poor health, marital failure, and social isolation imply a cutback in survival and reproductive fitness (Brown, et al. 2009; de Catanzaro 1995). As well, preferences for an altruistic spouse may lead to extreme levels of self-sacrificing traits through the runaway selection, and may be related to excessive guilt, shame, obsession with social acceptance, and fear of rejection (Nesse 2007). However, it is doubtful whether kin-level fitness improvement has taken place through these mechanisms in the past. In fact, among the relatives of the mentally disabled people, cognitive, executive, speech, and attention problems are more common than in general population (Sitskoorn, et al. 2004; Snitz, et al. 2005). According to some studies that directly assessed fitness using the TFR of relatives, some of them have shown that inclusive fitness increased (Bassett, et al. 1996; Haukka, et al. 2003; MacCabe, et al. 2009; Svensson, et al. 2007), and others show that there is no effect on inclusive fitness (Avila, et al. 2001; Srinivasan and Padmavati 1997). The results are inconclusive but do not seems to illuminate the paradox adequately.

Eighth, there is an attempt to explain as a heterozygote advantage. The asymptomatic heterozygous gene could benefit the individual (Huxley, et al. 1964; Karlsson 1978). If a heterozygote advantage or overdominance occurs, the dysfunctional trait located at multiple loci becomes difficult to be removed by natural selection. Due to the psychological characteristics of incest avoidance, the formation of homozygotes is restricted, and the removal of dysfunctional genes may be further delayed (Charlesworth and Charlesworth 1987). However, the heterozygote advantage is thought to be evolutionarily unstable, so it is not likely to cause long-lasting genetic variation (Bürger 2005; Keller and Miller 2006). Unless, by chance, the heterozygosity has the highest fitness (for example, sickle cell disease), it usually does not maintain polymorphism (Curtsinger, et al. 1994).

Ninth, according to the antagonistic pleiotropy hypothesis, there may be other benefits of genes that cause specific dysfunctional traits (Carter and Nguyen 2011). This theory is a trade-off hypothesis at the gene level. A compromise leads to balancing selection in which dysfunctional behavioural traits give benefits to individual or relatives (Figueredo, et al. 2006). For example, a phenomenon in which a particular gene has different costs and benefits for men and women is also an example of antagonistic pleiotropy (Rice and Chippindale 2001). However, it is still difficult to explain why the final TFR and survival rate does not increase. The heritability of defence activation disorder is relatively high, and numerous causative genes are distributed unevenly within the gene pool (Barton and Turelli 2004). Therefore, antagonistic pleiotropy is unlikely to occur in chronic multifactorial disorders. Antagonistic pleiotropy has limitations to explain the diversity of psychological traits.

Part II

Balancing selection is one of the evolutionary mechanisms to maintain the polymorphism of traits. Perhaps balancing selection could maintain the polymorphism of human behavioural patterns. Part 2 divides balancing selection phenomenon into niche specialisation and frequency-dependent selection and explain the key arguments and limitations of them.

To explain the evolutionary hypothesis of defensive activation disorder with a balancing selection model, an appropriate intermediate model should be formulated. MVT is an ecological model that explains the animal's migrations between patches, but it is also widely used to explain the movement of hunter-gatherer societies. Part 2 suggests that the level of defence activation among individuals can be transformed into computable ecological currency by using MVT for construction agent-based evolutionary simulation model of defence activation disorder.

1. Balancing Selection

Recently, a model of balancing selection has been presented as a compelling explanation about the diversity of behavioural patterns. The model asserts that polymorphism can be maintained by natural selection with eco-evolutionary dynamics (Travis, et al. 2014), even under the situation of no repetitive mutation, no gene flow, and no genetic drift. It has been supported by geneticists in the United States, including Theodosius Dobzhansky, and British ecologists (Futuyma 2013). The heterozygosity advantage phenomenon mentioned in the previous section is also one example of balancing selection, even though it is hard to apply to defence activation disorder.

This model can be roughly divided into the niche specialisation and the frequency-dependent selection (Bergmüller and Taborsky 2007; Roff 1997), which are not mutually exclusive concepts. In fact, one of the above-mentioned hypotheses does not rule out another hypothesis too. Each model has a different standpoint as well.

Niche specialisation refers to the phenomenon by which each within a habitat adapts to a variety of niches (Dall, et al. 2012; Montiglio, et al. 2013b). It is the case that different genotypes are best adapted in different microhabitat environments, i.e., multiple-niche polymorphism. This phenomenon is more apparent when soft selection occurs. That is, the situation of a specific place does not affect the absolute fitness of the individual, but only the relative superiority of individuals with one particular genotype (Futuyma 2013). This diversifying selection by superior fitness could maintain phenotypic polymorphism and possibly explain the various activation levels of defence modules.

Habitat consists of various patches made up of different biological or non-biological conditions. An individual may occupy only a subset of the ecological niche that the entire population inhabits (Araújo, et al. 2011; Bolnick, et al. 2002). The amount of resources provided by each ecological patch depends not only on the distribution of food resources but also on the risk of attack by predators, the rapidity of resource exhaustion, the difficulty of acquiring resources, and the reproduction and survival competitiveness

of populations lodging the same patches (Davies 2014; Kelly 2015). Therefore, each develops a variety of adaptation strategies that fit the given niches (Araújo, et al. 2011; Bolnick, et al. 2002). Since the frequency of individuals who employ in a behavioural strategy cannot be ecologically uniform in all habitats, niche specialisation can be indirect preconditions that lead to the frequency-dependent selection.

The fitness of a phenotype can be determined by the frequency of the individual exhibiting the phenotype in the population. The frequency-dependent selection is a phenomenon by which, in various ecological situations, the frequency of individuals with a particular trait is maintained continuously through interrelationships among individuals (Bergmüller and Taborsky 2007). Frequency-dependent selection may be caused by interactions between individuals with different behavioural traits, or indirectly by their relative fitness to environmental conditions.

There have already been attempts to explicate MDD using the frequency-dependent selection model. Various aspects of MDD can be explained by involuntary subordinate strategies. Taken as a whole, subordinate strategies are overall associated with lower fitness but can be maintained as an evolutionarily stable strategy (ESS) depending on the frequency of population groups (Maynard Smith and George R 1973). As more individuals become submissive, dominant individuals become more profitable. When there are more dominant individuals, the submissive individual becomes more favourable. In this condition, infrequent phenotypes have higher fitness (the inverse frequency-dependent selection). Although it is a compelling argument, it cannot apply to solitary animals. It is also questioning to explain general anxiety, fear, panic, and defensive obsession because they sometimes occur regardless of interpersonal struggle or positional competition (Sloman, et al. 2003). However, the hierarchical relationship is not a prerequisite for the frequency-dependent selection. This may be caused by direct interactions between individuals with different behavioural traits but may occur indirectly, for example, by different population density among discrete ecological regions, as mentioned later.

In addition, research has recently been published that considers mental disorders at the genetic level as a result of balanced selection. Thr136Ile variant of the SLC18A1 gene encoding the vesicular monoamine transporter 1 (VMAT1) protein was positively selected by balanced selection in the non-African population. It would be happened about 100,000 years ago (Sato and Kawata 2018).

In the case of the ideal free distribution model, there are resource-abundant places as much as necessary, and individuals can leave and stay in any place freely. The population is increased in the affluent area. On the other hand, the population decreases in the resource-poor area. As a result, the resource acquisition rate becomes the same. Thus, the value of resources per individual in the former area and the latter area will eventually decrease equally (Fretwell 1972). If the population excessively grows in the resource-rich area, the individual living in a resource-poor area becomes relatively advantageous. The opposite is also exact. Depending on the amount of resources and population in the niche, the relative fitness of individuals is frequency-dependently determined.

Thus, behaviours that lead to dysfunctional responses can be adaptive behavioural strategies in the circumstance of a specific niche, and the genotype associated with the dysfunctional behavioural pattern can be maintained in a frequency-dependent manner for a long time in the gene pool. Perhaps defence activation disorders could be the result of multiple-niche polymorphism. However, this leads to the question of how emotional and cognitive features of depressive disorder, anxiety disorder, and obsessive-compulsive disorder have to do with the ecological situation.

2. Estimating the Resources and Defence Activation

Aaron Beck mentioned automatic, spontaneous, and uncontrollable negative thoughts about oneself, the world, and the future as one of the cognitive characteristics of depressed patients (Beck 2009). They called it the cognitive triad (Beck 1997). A

similar cognitive tendency is observed in individuals with anxiety disorders (Clark 2009). Emotion, anxiety and cognition are deeply related to each other. Three cognitive distortions point to different entities, but they can be abridged in one schema. It is a belief that the ego will not get much from the world in the future. The cynical view toward the ego, the world, and the future can trigger psychomotor inhibition (Beck 1997). A negative cognitive schema leads to inhibitory behaviours such as losing earlier, staying longer and stopping seeking. So negative cognition makes the individuals avoid challenges and remain in situ.

Emotion is not only a subsequent phenomenon evoked by the cognition but also a mediator that guide the cognitive judgement. Moreover, emotions are often activated at the unconscious level, without any cognitive awareness. Evolutionally, feelings are older than the thoughts. The evolution of emotions could date back to the early stages of life (Damasio 2019).

In other words, emotion may also operate as superordinate cognitive programs that appraise what the ego can obtain from the world in the future, known as the average resource acquisition rate in the entire habitat (Cosmides, et al. 2005). It is impossible to obtain information on the resource acquisition rate of many patches in all habitats or to calculate the average value thereof. This assumption is in line with Tooby and Cosmides's argument that emotions exist to orchestrate other subordinate cognitive programs to achieve the best consequence of any given situation (Tooby and Cosmides 2009). For example, depression may be an emotional condition intended to rethink current behavioural strategies and curtail them if needed (Cartwright 2016).

How are the hypothetical models about defence activation disorder it designed, and proven or rejected in the sense of ultimate causation? It is tough to establish an evolutionary ecological model of portraying psychological phenomena such as emotions because there is no concurred way to quantify emotional levels. 'A's mood is 20 per cent more depressive than B's mood' is not scientific but just rhetorical. However, turning inner emotions into external behaviours can provide more clarity. The benefits and costs

of behavioural patterns can be quantified by using ecological currencies. However, it is usually not possible to measure, directly, the fitness consequences of a particular behaviour. The alternative is the use of proxies (Vasconcelos, et al. 2018). The resource could be a reasonable candidate for the ecological currency because the amount of resources acquired is usually linked to survival or reproduction (Vasconcelos, et al. 2018). Thus, an optimal model can be designed for how reproductive fitness diverges depending on the emotional levels, precisely defence activation level.

Let us think of individuals in an ecological environment. Individuals who feel potential threats (such as attacks by predators, depletion of residual resources, conflicts and position competitions due to increased populations, and the shrunken prospect of reproduction) may activate defence modules (Sih, et al. 2004; Székely, et al. 2010). What strategies can be employed by individuals with activated defence modules?

First, individuals can leave the niche with a high diminishing rate of return and search for a new ecological niche. For example, individuals can move to a patch with abundant resources and no threats from predators. Alternatively, they can defeat other competitors to monopolise the patch and redouble the return (Araújo, et al. 2011). At any rate, achieving enough total reproductive fitness matters. In both cases, the defence mechanism need not be activated.

Second, individuals may remain at their patch for a longer time. This strategy works under the condition of gloomy prospects; in other words, ‘wait until spring’ (Araújo, et al. 2011). It is the strategy of choice if the cost or risk of moving to a new patch is enormous.

According to the MVT, the decision between the two strategies depends on the cost of moving to the new patch (Charnov 1976). The patches here do not mean just spatial patches; patches are distributed in the infinite temporal and spatial space. If it provides an individual with diverse reproductive success, it should be regarded as a different patch (Réale and Dingemanse 2010).

The MVT is a model for explaining behavioural strategies that maximise the long-

term acquisition rate in a patch environment where resources are widely distributed. Originally, MVT was proposed as a mathematical model to explain the optimal foraging strategy of animals, but it is also useful in explaining various human behavioural strategies (Kelly 2015).

In a patch occupied by an individual, if the rate of resource acquisition per unit time is reduced, it is helpful to leave and find a new patch. However, if a new promising patch is far in the distance or there is high uncertainty about the resource acquisition rate of new potential patches, staying in the current patch is a better choice (Nesse 2019). The optimal moment to leave for a new patch depends on the marginal resource acquisition rate of the current patch, the average resource acquisition rate of the entire habitat, and the expected movement cost or travel time (Fig. 1) (Charnov 1976).

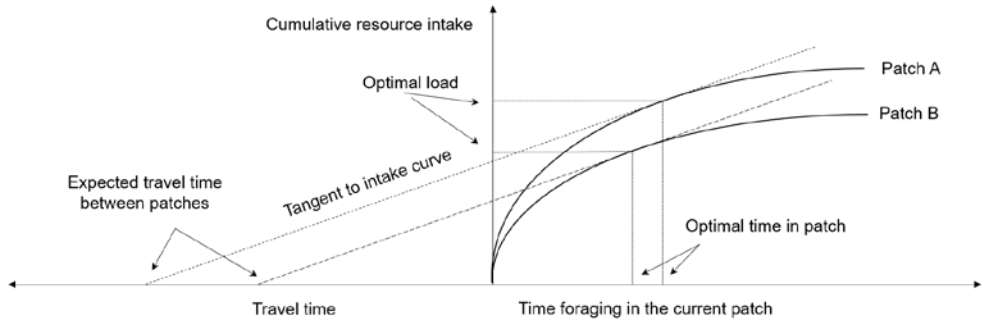

Figure 1 A Graphical Representation of the MVT (travel time reflects movement cost).

The resources of a patch *(i)* decrease gradually because the individuals continually pick up them. Since the individuals pick up easy-to-acquire resources first, the resource acquisition per unit time (*T*) - that is $h_i(T_i)$ - also decreases gradually. Each patch has a different $h_i(T_i)$. In Patch A with a high $h_i(T_i)$, the rate of the resource returns declines slowly (solid line A). On the other hand, in Patch B with a low $h_i(T_i)$, the rate of the resource returns declines rapidly (solid line B).

Then, the optimal time to leave the patch, uTi, which is the sum of the time spent in the patch (*i)* and travel time (*t)*, is:

$$uTi = t + Ti$$

[where t = average time to search and move to the new patch; Ti = time spent in the current patch i (i = 1, 2..., k)]

The mean rate of resource acquisition, that is ${}_nE_i$, during the time spent in patch *i* and while moving to the next patch can be expressed as:

$$nEi = (hi(Ti) - t \times ET) / uTi \quad = (hi(Ti) - t \times ET) / (t + Ti)$$

[where ET = cost per unit time to explore and move to new patches*; hi(T) = the amount of resources acquired per unit time, T, from the patch (i = 1, 2..., k); hi (Ti) = resource acquisition per unit time in patch i (i = 1, 2,..., k)]*

When the equation is differentiated by the time spent in the patch, *T*, the slope of the resource return obtained at a specific time in a patch is as follows:

$$\partial hi(Ti) / \partial Ti$$

Therefore, when the rate of resource return obtained at a specific time at a patch become equal to or smaller than the average return of the resource in the total habitat, *h total(T)*, that is if $\partial hi (Ti) / \partial Ti - h\ total\ (T) < 0$, the agent should leave the current patch.

When the value of $\partial hi (Ti) / \partial Ti - h_{total} (T)$ approaches zero, the defence module would be activated. The reduction in the resource acquisition rate is the critical ecological pressure that directly affects the survival and reproduction of individuals. In Fig. 2, it is advantageous for individuals in the patch A to stay there longer than individuals in the patch B, because the resource acquisition rate decreases more slowly in the patch A

than in the patch B. In other words, the defence module should be activated more quickly and robustly in resource-poor patches (Fig. 2). This logic is consistent with results of clinical studies that defence activation disorders occur more often in the unfortunate socioeconomic situations such as high competition, socioeconomic crisis, high unemployment rate, and natural disasters (Allen and Badcock 2003; Mucci, et al. 2016; Nolen-Hoeksema and Morrow 1991; Uutela 2010; Wang, et al. 2010).

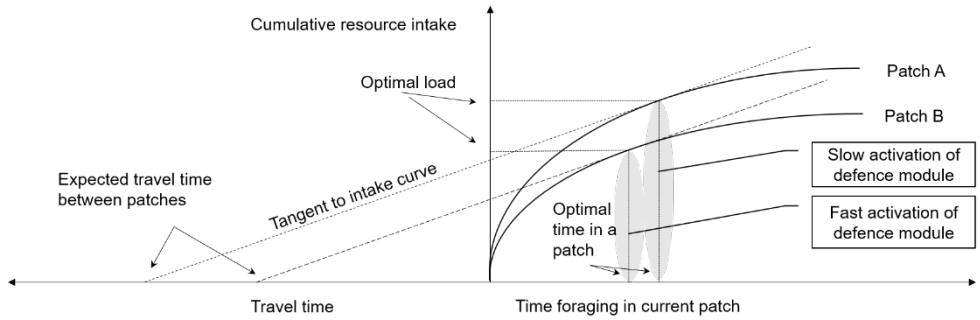

Figure 2 A Graphical Representation of the Activation of Defence Module and the Resource Acquisition Rate (travel time reflects movement cost).

As mentioned above, the optimal time to leave the patch is determined by $\partial h_i(T_i) / \partial T_i - h_{total}(T)$. The agent in the patch already knows *the* $hi\ (Ti)$ and Ti. However, information about $h_{total}(T)$, the average resource acquisition rate in a given habitat, cannot be obtained accurately at the individual level.

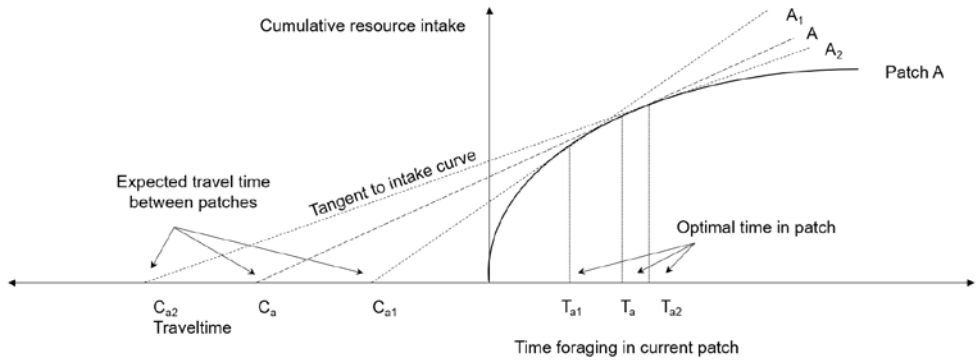

Figure 3 Optimal Time to Spent in the Current Patch depending on Movement Cost

In Fig. 3, let C_a be the initial value. Then, the x-axis value T_a, where the dashed line A touches the marginal value curve, is the optimal time to remain in the current patch or the cost of remaining in the current patch. However, the cost (or risk) of leaving to a new patch is relatively small for $C_{a1}(T_{a1} < T_a)$. In this case, even if the cost of seeking a new patch is added, movement can increase the average return of the agent. Therefore, it is advantageous to move to another patch after T_{a1}, whereas the cost (or risk) of C_{a2} moving to a new patch is relatively higher than that of C_a. Therefore, it is advantageous to stay longer in the current patch ($T_{a2} > T_a$).

However, when the actual $h_{total}(T)$ is the slope of the dashed line A, if the agent misinterprets it as the dotted line A_1, the agent leaves the current patch earlier than the optimal time and moves to a new patch. In this case, the agent underestimates the cost (or risk), for leaving to a new patch. By contrast, if the agent misinterprets it as the dotted line A_2, it leaves the current patch later than the optimal time. In this case, the agent overestimates the cost (or risk), for leaving to a new patch.

Let d be the weight of the individual for $h_{total}(T)$. Therefore, the weight of average resource acquisition per unit time, $weighted\ h_{total}(T)$, can be expressed as:

$$weighted\ h_{total}(T) = h\ total(T) \cdot (1 - (d-1))$$

$$[\ 0 < d < 2,\ mean\ of\ d = 1,\ 0 < d < 2\ ]$$

Here, d is assumed to be a normal distribution with an average of 1, a maximum value of 2, and a minimum value of 0. In other words, an individual in a patch will try to leave the patch when $\partial h_i(T_i) / \partial T_i - h_{total}(T) \cdot (1 - (d-1)) < 0$. Here $d > 1$ means that the agent is more pessimistic than the actual condition of the entire habitat, and $d < 1$ means that the agent is more optimistic than the actual condition of the entire habitat. Thus, d

is greater than 1 for D-type disorders and *d* is less than 1 for d-type disorders.

These are summarised as follows. The amount of resources in various patches of the habitat are diverse. The optimal leaving time varies depending on the amount of resources and the diminishing rate of returns in each patch. In order to determine the optimal time for leaving, the individual must accurately estimate the average amount of resources and the average diminishing rate of returns in the entire habitat. However, it is an impossible cognitive task. Thus, emotions can be used as psychological appraisal tools for the ecological prospect of the habitat. It is a satisficing strategy based on the bounded rationality assumptions. Individual's decisions cannot be perfect because of the limitations of cognitive capacity and the lack of information (Cartwright 2016; Simon 1957). Of course, if the environment is uniform in time and space, the emotion as a superordinate cognitive module will gradually make an optimal judgment. However, if the habitats are different patchy environments in time and space, the constant optimal value cannot exist. Therefore, individuals with various levels of defence activation may exist together. How can these assumptions be proven?

So far, the following arguments have been done in chapter 1. Defence activation disorder is a paradoxical evolutionary phenomenon. Several anthropological hypotheses have been presented to illustrate the ultimate evolutionary explanation of the dysfunctional behavioural patterns. However, most of these hypotheses are intricate to be proved or disproved because quantifying the outcomes of dysfunctional behavioural patterns or combining the inner emotions with the behavioural patterns is tricky. As far as I know, agent-based modelling (ABM) for evolutionary explanations of mental disorders has not been used for the research of evolutionary psychiatry. Very recently, Randolph Ness commented on one case of it in 2019 (Nesse 2019). By applying the MVT, numerous emotional patterns of defence activation disorders such as MDD, anxiety disorder, and OCD can be switched into quantified behaviour patterns. In the simulation environment, the amount of resource acquisition can be set easily. Also, by converting the amount of resource acquisition into survival or reproductive success, an

evolutionary agent-based simulation model can be constructed.

In this study, I will suggest that, under a variety of environmental conditions, defence activation level deviated from the optimal global value, as determined by the MVT, can be the ESS by the scientific tool of Agent-Based Modelling (ABM). Chapter 2 summarises the research questions of anthropologic interests. Chapter 3 describes the methods in detail, especially the reliable simulation algorithm of the evolutionary agent-based model to systematically deal with the research questions. Technical parts of the research are summarised in supplementary information behind the paper. Chapter 4 presents the results of the study as follows: First, the reliability and feasibility of the defence activation disorder simulation model. Second, the niche specialisation and frequency-dependent selection in the simulated environment are demonstrated. Third, it is described how some environmental conditions such as movement cost, environmental heterogeneity, and fluidity affect the fitness of individuals with different defence level. Fourth, time-series consequence with the change of environments are presented concisely. In chapter 5, the implication of the research methodology results is discussed. Moreover, it is discussed how the balancing selection model and the mismatch hypothesis can be applied to elucidate the nature of defence activation disorder, followed by the limitations and the research direction of the future. In chapter 6, the whole story was summarised again.

Chapter 2. Research Hypothesis

1. The Main Hypothesis

> The primary alternate hypothesis of this study is that a range of dysfunctional behavioural strategies with different levels of defence activation can be maintained as ESS within the agent-based evolutionary simulation environments by the evolutionary mechanisms of balancing selection only when the gradient distribution of resource exists (H_1).
>
> Therefore, the null hypothesis is that a range of dysfunctional behavioural strategies with different levels of defence activation cannot be maintained in any case or can be maintained regardless of the gradient distribution of resource (H_0) within the agent-based evolutionary simulation environments.

In order to verify these hypotheses, we assume the following three environments. In the first environment, the resources are uniformly distributed both spatially (E_1). In the second environment, resources are not distributed spatially uniformly, but are randomly distributed throughout the environment (E_2). In the third environment, resources are not uniformly distributed in space, and resources are distributed in a gradient in accordance with a certain spatial tendency in the entire environment (E_3).

If a range of dysfunctional behavioural strategies with different levels of defence activation can be maintained only in E_3, the null hypothesis can be dismissed. Otherwise, we cannot prove the alternative hypothesis. Otherwise, the alternative hypothesis cannot be verified in an evolutionary simulation environment.

Under the main hypothesis, the following research questions are proposed. By the order of the model design, the questions about the reliability and feasibility was proposed

first and then the questions about main hypothesis was proposed.

1.1 Reliability and Feasibility of the Model

1.1.1 The agent-based simulation model of the defence activation disorder using the MVT presents different timings of leaving according to each agent's defence activation level (*d-value*)?

1.1.2 Does this simulation model maintain the stable range of the global *d-values* over time? Does the proportion of agents with different *d-values* evolutionary keep stability?

1.1.3 Does the model persist enough to reflect the long evolutionary epoch? Are variables stable and predictable for a long time?

1.2 Niche Specialisation and Frequency-Dependent Selection

1.2.1 Is the null hypothesis rejected? What are the differences between the three environmental conditions (E_1, E_2 and E_3)?

1.2.2 Is population density proportional to the amount of patch resources ?

1.2.3 Are the local *d-values* differentially distributed according to the amount of local resources? Do the distributions of agents with different *d-values* vary depending on the amount of local resources? Are they negatively correlated with each?

2. Several factors affecting the level of defence activation

In addition to the main hypothesis, I have identified potential factors that affect the proportion of individuals with different *d-values* in the population. I also posed the following question as to what evolutionary phenomena can be emerged with time, and what clinical implications can be made in relation to the mismatch hypotheses.

Specifically, the following research questions are proposed.

2.1 Several Factors affecting *d-value*

2.1.1 Does the difference in the movement cost cause variations in the *d-value* of the population? Which of the agent with over-activated defence level and under-activated defence level have differential fitness under the situation of different movement cost?

2.1.2 Does the difference in the reproductive cost cause differences in the *d-value* of the population? Which of the agent with over-activated defence level and under-activated defence level have differential fitness under the situation of different reproductive cost?

2.1.3 Does the difference in the environmental heterogeneity cause differences in the *d-value* of the population? Which of the agent with over-activated defence level and under-activated defence level have differential fitness under the situation of different environmental heterogeneity?

2.1.4 Does the difference in distance of movement at a time (fluidity) cause differences in the *d-value* of the population? Which of the agent with over-activated defence level and under-activated defence level have differential fitness under the situation of different socioecological fluidity?

2.2 Temporal Changes and Mismatch Phenomena

2.2.1 How does the global d -values react when movement costs and reproductive costs over time?

2.2.2 How do the proportions of agents with different *d-values* change when movement costs and reproductive costs over time?

Chapter 3. Method

The method is divided into three parts. First, the entire simulation model is described. Sub-models are also described in detail. Second, the whole algorithm and program interface of NetLogo is presented. Third, the parameter calibration of the model and the full codes with the model is described in a standard way (Wilensky 1999). For convenience, the full description of the third part is presented in the supplementary information section.

What is ABM? It is a type of model. The model is a simple purposeful representation of complex real-world (Starfield, et al. 1990). Individual-based model (IBM)or ABM is to focus the individual agents interacting with each other and their environment locally for time-serially (Grimm, et al. 2006). ABM is the across-level model that are fruitful for solving the emergence phenomenon (Railsback 2012). It has been applied to a varied of scientific fields, for example, ecology, economy, sociology, psychology, meteorology, archaeology, etc. So, it could be one of the promising methodologies for evolutionary anthropological researches, because gene, internal psychology, individual behaviours and interaction between them in an ecological environment through the geological timescale should be considered together for the study of neuro-anthropology. Unfortunately, ABM is in its infancy in the field of anthropology now.

Generally, assistance with a computer technology is essential for ABM, because it requires a vast number of repetitive mathematical operations. Several scientific programming tools for ABM have been developed. There are some experimental platforms for ABMs, i.e. Swarm, Repast, MASON, Ascape, Breve, PS-I, and so on. Meanwhile, NetLogo is one of the most widely used platforms because it is an user-familiar programming language with powerful functions for analysis and virtual graphical interface for grasping what is going on the simulated world (Wilensky and Rand 2015). So, the agent-based model of defence activation disorder in this study is coded with the

NetLogo language.

1. Model Description

The agent-based model of defence activation disorders via the MVT was programmed using NetLogo (Wilensky 1999). Model description followed the ODD (Overview, Design concepts, Details) protocol (Grimm, et al. 2006; Grimm, et al. 2010). The abbreviations used in the model are as follows (Table 2).

Table 2 The Abbreviations used in the Marginal Value Model of Defence Activation Disorders

Abbreviation	Meaning
C.C.	Carrying Capacity
d-value	Level of d. It ranged from 0 to 2, and the initial average is 1.
E	Energy. The amount of energy in each circle.
E_0	Initial Energy.
Env.Ht.	Environmental Heterogeneity. The linear distribution of the amount of resources in the patch, the average amount of resources is mean E_0, and the width of resources varies according to Env.Ht.
ht.w	Weighting factor for Env.Ht.
Int.No.	Initial Number. The population of circles at the beginning of the simulation.
M.E.R.	Minimal Energy for Reproduction. It includes the energy for nurturing.
mer.w	The weighting factor for M.E.R.
Max.D.	The maximum distance which circles can move at a time. It represents the socioecological fluidity.
Mnt.Cost	Maintenance Cost.
Mov.Cost	Movement Cost.
mov.w	The weighting factor for Mov.Cost

M.R.D.R.	Mean Rate of Diminishing Returns.
NA	Agents with neutral defence module
OA	Agents with overactivated defence module
R	Resource. The amount of resource in each patch.
R_0	Initial Resource. The original amount of resources.
R.D.R.	Rate of Diminishing Returns.
Rep.Prob.	Reproductive Probability.
R.O.P.	The ratio of Occupied Patches.
Local R.O.P.	The ratio of Occupied Neighbouring Patches.
TFR	Total Fertility Rate
TSS	Time Span of Staying in the current patch before moving to another patch.
TT	Transit Time for the lifespan
UA	Agents with under-activated defence module

1.1 Overview

Purpose

The purpose of the agent-based model of defence activation disorders is to determine whether diverse activation levels work as ESS, even though they are sub-optimal in the context of the entire environmental condition. The model aims to demonstrate the phenomenon that the proportion of individuals with high *d-value* and low *d-value* maintains stable under various patchy environment. Additionally, the factors affecting the proportion of individuals with high or low *d-value* are analysed.

Entities, State Variables, and Scales

This model has two kinds of entities: the people, which are represented as circles (movable agents), and the ecological niches, which are represented squared patches (fixed agents) in the two-dimensional squared environment reflecting the entire habitat.

The model is spatial: the patch consists of 1369 square grid environments (37 x 37). In this model, patches with spatially unequal resource level are arrayed on a two-dimensional plane. Only one circle can be placed in a patch. Patches do not just mean the spatial place, but also refers to the various environmental conditions within entire habitat (Fig. 4).

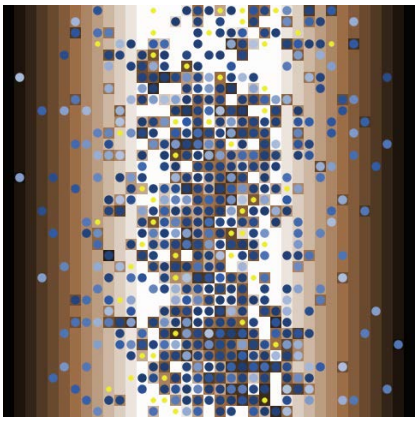

Figure 4 The Simulated World of the Model.

Each patch has two important state variables: the R_0, the R. The circle can get information about the R from the patch. The amount of resources is distributed differentially, according to Env.Ht. The distribution is vertically uniform and horizontally gradient. R_0 of patches arranged from the lowest to the highest through x-coordinates. The average amount of resource is set as 150 (at xcor 9). When Env.Ht. is 1, the resource amount of patch with xcor 0 is 300, and the resource amount of patch with xcor 18 is 0. If Env.Ht. is 0, the resource amount of patch with xcor 0 is 150, and the resource amount of patch with xcor 18 is also 150. If Env.Ht. is 2, the resource amount is distributed from -150 to 450. The details are explained again in the section of sub-models.

The circle has state variables of age, E_0, E and *d-value*. The Int.No. and the E_0 of the circle is set at the initial setting. A circle represents each movable agent on the interface screen, and a new-born circle is displayed in yellow for one year. Movement between patches means leaving to a new ecological patch, and the energy required to

movement corresponds to Mov.Cost.

The model runs at a yearly time step. Each circle survives for up to 25 years, reflecting the reproduction period from 15 to 40 years of age. Anthropologically, children aged 15 or younger are hard to give birth without potential health problems and acquire enough resources for nurturing by themselves (Trevathan 2010). Resources for survival to age 15 are included in M.E.R. Also, although individuals after age 40 can increase inclusive fitness through additional production, this is purposefully disregarded for the simplification of the model. The circle of the model has no gender. Time-span of simulations reflect mainly 5 or 10 kiloyears (kyr).

Process overview and scheduling

The model includes the following actions. They are performed in the order listed at each time step.

Energy Acquisition and Maintenance

The circle acquires resources from the patch. The E increases by multiplying the patch's resources by R.D.R. The default value of R.D.R. is 0.3. The R of the patch is reduced by the same amount which the circle gets. Moreover, the E of the circle falls by Mnt.Cost. If the circle's E reaches below 0 or the age exceeds 40, the circle dies. Died circles are removed from the environment at the beginning of the next step.

Decision of Movement

The circle moves to another patch if the expected amount of energy acquisition on the patch is less than the expected amount of average energy acquisition in the entire habitat in addition to Mov.Cost and if E exceeds Mov.Cost (Charnov 1976). At this time, the expected average amount of energy acquisition in the entire habitat is calculated by weighting the *d-value* of each circle on the actual amount of average energy acquisition.

If the circle does not move, the TSS of it increases by 1. When a move is completed, the TSS returns to zero.

Movement

The circle moves randomly to one of the neighbouring patches. If there are no empty patches in 8 neighbours, the circle stays. If movement becomes successful, Mov.Cost is paid from E (See sub-model).

Decision of Reproduction

If the age is between 15 and 40 years old, the E of the circle is higher than M.E.R. weighted by (1 - Rep.Prob.), and there are empty patches among neighbours, the circle breed a new offspring. The new-born circle begins the life at one-of neighbouring patches. If there are no empty neighbouring patches, the circle waits for the next chance. The *d-value* assigned to the new-born circle is set by multiplying the parental *d-value* by a randomly determined number in the distribution with an average of 1 and a standard deviation of d (SD-of-d). Here, Rep.Prob. is determined by the logistic function. Details are provided in the section of sub-models.

1.2 Design Concepts

Basic Principle

The basic principle of this model is about the fitness of agents with sub-optimal *d-value*. The purpose of this model is to determine the usefulness of the MVT for explaining the relationship between *d-value* and distribution of R, Mnt.Cost, Mov.Cost, and M.E.R. within various simulation environments. It is also to identify whether dysfunctional behavioural patterns associated with defence activation disorders can be maintained as ESS within simulated evolutionary environments.

Emergence

The results that emerge from the model are the E of circles, TFR, mortality, average *d-value* and distribution of circles according to the *d-value*.

Adaptation

Adaptive behaviour of circles are judgements of movement. Circles adapt to the local environment through generations by differential survival and reproduction. The *d-value* of each agent limit their adaptive behaviour and their behaviours modified *d-value* of themselves by generations. Breeding and death are determined by the R and the availability of empty surrounding patches. So, population density and resource amount in local environment restraint the circle's behaviours indirectly.

Objective, Learning, Prediction, Sensing and Interaction

The objective is to maximise the final currency, i.e., the TFR. Learning or prediction is not included in the model. Each agent can perceive the amount of resource acquisition as well as its diminishing rate and the average amount of resource acquisition per unit time of the entire environment adjusted by the *d-value*. Here, the average amount of resource acquisition per unit time perceived by circles is not accurate because circles cannot sense it. Moreover, circles cannot perceive any other information about the environment, patches, or other circles even whether there are empty neighbouring patches around them. Interaction between the patches is not considered in the design, but they can affect other circle's behaviours through the crowdedness.

Stochasticity

The stochasticity of the model is as follows. The new patch for movement or reproduction and *d-value* of each circle are determined stochastically in an ecological environment. Also, in the initial setup, the placement of the circles is determined randomly. In the real-world, circles may have some information about the amount of

resources of neighbouring patches from their experience or a social network.

Moreover, all individuals have different competencies about movement efficiency, survival, and reproduction. However, the model does not consider asymmetric information levels or differences in physical or psychological capabilities between individuals for simplification. The model was designed based on the killjoy explanation, to say, intricate behavioural patterns could be produced by simple mechanisms (Dennett 1983; Shettleworth 2010a; Shettleworth 2010b).

Observation

Through the interface window, the behaviours circles, individual state of E, the distribution of R and number of new-born circles can be observed in real time. There are 13 plot charts, for example, No. of circles, Mean TSS, Mean R, TFR, Total net E for lifespan, TT, Total Mnt.Cost for lifespan, Total Mov.Cost for live span, mean lifespan, mean age, the proportion of OA and UA, R.O.P and *d-value* (mean and SD). Some of them offer 4 different results per charts according to their *d-value* (UA, NA, OA). They can be observed in real time. Also, there are 4 histograms for age, E, R, *d-value*. Also, a specific number of them are monitored in real time. All of them are presented the supplementary information section.

1.3 Details

Initialization

The model initiated with 400 circles, but the population of circles can be modified from 1 to 1369 (Int.No.). The number 400 is an arbitrary number, but it is intended to reflect the magic number 500 of typical hunter-gatherer societies (Sellet, et al. 2006). The number 400 is close to the 475 people considered as the natural reproduction population size {Kelly, 2015 #1843}. However, because it did not reflect the population under 15 and over 40, 400 circles were supposed to be enough number above the

minimum population size to withstand short-term fertility and mortality changes (Wobst 1974).

Circles located at the centre of each patch randomly. Colour of circles is blue; the more energetic they are, the lighter their colour is. However, new-born circles coloured yellow for one year. The initial energy level (E_0) of the circle can be adjusted up to 200, but the initial default value is a mean of 50 (0 ~ 100). The R.D.R. and M.R.D.R. of each patch can be within 0 and 1. Mov.Cost. can be set from 0 to 100, but the initial default value is 7. Mnt.Cost can be within 0 and 100, but the initial default value is 20. The Env. Ht. is 1, but it can be adjusted from 0 to 2. The C.C. can be up to 1500, but the initial default value is 900. M.E.R. may reach 400, but the initial default value is 130. The *d-value* of the parent mostly determines the *d-value* of the offspring. The model is designed to give birth to one to three offspring for a lifespan. It reflects two to six offspring because parents in this model to give birth to a 15-year-old offspring. Indeed, childhood mortality rates in hunter-gathering communities range from 50 to 60% (Gurven and Kaplan 2007; Hewlett 1991). Innate *d-value* is determined by parent's *d-value* multiplied by the number randomly selected from the normal distribution with an average of 1 and a standard deviation of d (SD-of-d). The default value of SD-of-d is 0.03.

Input data

This model uses no time series inputs.

Sub-models

Energy Acquisition and Maintenance

Let R_0 be the initial resource amount of each patch. In each patch, the circle acquires resources as energy. Energy acquisition and Mnt.Cost are set as follows:

$$E_1 = E_0 + R_0 \times R.D.R. \quad (0 \leq R.D.R. \leq 1)$$

Each patch also loses the same amount of resources. Also, each circle loses

Mov.Cost. (if move) and Mnt.Cost. When k times are repeated, the amount of final energy obtained is as follows:

$$E_k = R_{k-1} \times R.D.R. - (Mov.Cost. + Mnt.Cost.),\ (k \geq 1)$$

Let R_k be the amount of resources remaining in the patch after *k* repetitions, as follows:

$$R_k = R_0(1 - \sum_{n=1}^{k} R.D.R.^n) - (Mov.Cost. + Mnt.Cost.),\ (k \geq 1)$$

This can be reflected as follows:

$$E_{n+1} = En + (Rn \times R.D.R.)$$

$$R_{n+1} = Rn - (Rn \times R.D.R.)$$

$$E_{n+1} = En + (Rn \times R.D.R.) - Mnt.Cost.$$

Gradation of Resource Distribution

When the coordinates of the centre patch are (0.0), the habitat has a square structure with 37 vertical and 37 horizontal patches. If the coordinates of a patch are (X, Y), it has a value of R_0: 300 minus the absolute value of X divided by 18 multiplied by 300. If the X value is 0, the resource is 300, and if the X value is 18, the resource is 0 (default). It is calculated as follows.

$$R_{pxcor(x)} = Mean.R_0 \times (Env.Ht. \times ht.w + 1) - \frac{|x| \times Env.Ht. \times ht.w \times Mean.R_0 \times 2}{18}$$

As mentioned above, the structure of the habitats is designed as a continuous torus of revolution.

Movement Cost

Mov.Cost is a value obtained by multiplying Mov.Cost by the average number of movements. Here, the average number of movements is determined as below. The mobility is different depending on the micro-environment, but it is simplified to be determined by the occupancy of the entire habitat. Thus, Mov.Cost is calculated as

follows (sub-model 1):

$$\sum_{k=0}^{\infty} Mov.Cost \times R.O.P.^{k}$$

$$= \lim_{n\to\infty} \sum_{k=0}^{n-1} Mov.Cost \times R.O.P.^{k}$$

$$= \lim_{n\to\infty} \frac{Mov.Cost.(1 - R.O.P^{n})}{1 - R.O.P}$$

$$= \frac{Mov.Cost.}{1 - R.O.P.}$$

Movement Decision

The movement of the circle is determined as follows. If the proportion of the patches occupied by the circle is R.O.P., n = the number of all patches and *Y* – $\boldsymbol{U}([0,1])$*;*

$$age \leq 40, E > M.E.R., Y > R.O.P.$$

and if the following conditions are satisfied, the circle moves.

$$R \times (1 - R.D.R.) - \frac{Mov.Cost}{1 - R.O.P.} < R.D.R. \times \frac{\sum_{1}^{n} R(p_n)}{n} \times (1 - (d - 1))$$

Here, $R(p_n)$ is the amount of resources in the n_{th} patch.

Reproductive Probability

Reproductive probability is calculated as follows. When the population (X_1) is 50% of the carrying capacity (C.C.) of the entire habitat, the likelihood of reproduction is P_1; when the population (X_2) is 100% of the C.C. of the whole habitat, the likelihood of reproduction is P_2. Then, intermediate variables A and B can be obtained as follows:

$$A = ln\left(\frac{P_1}{1 - P_2}\right) - \left(\frac{ln\left(\frac{P_1}{1 - P_2}\right) - ln\left(\frac{P_2}{1 - P_1}\right)}{X_1 - X_2} \times X_1\right)$$

$$B = \frac{D - C}{X_1 - X_2}$$

Here, Rep.Prob. for the given population number X is as follows:

$$Rep.Prob. = e^{(A+B\times X)}$$

If the object capacity is 500, P_1 is 0.7, and P_2 is 0.2, the logistic function of the probability of reproduction can be expressed as shown in the following chart (Fig. 4).

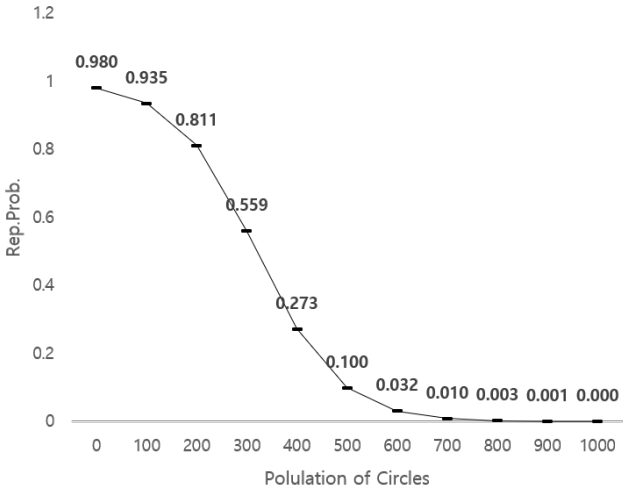

Figure 5 Logistic Function of Rep.Prob.

The circle's d-value

In the initial state, the *d-value* of a circle is determined as follows:

$$D \sim U([0.5,1.5])$$

Each agent is classified as an Overactivated Agent (OA), a Neutral agent (NA), or an Under-activated agent (UA) depending on *d-value*. Therefore, they are classified as follows (SD is 0.15):

$$Z > 1 + SD : OA$$

$$Z \leq 1 + SD \ and \ Z > 1 - SD : NA$$

$$Z \leq 1 - SD : UA$$

2. Parameter Calibration

The main parameters of this simulation model are as follows: R.D.R. (and M.R.D.R.), Env.Ht., Mov.Cost, Mnt.Cost, SD-of-d. If the setting is extreme, all circles will behave the same way. For the stable proceeding of the simulation model, the limits of each parameter were calibrated. Also, the stress tests were performed for several hundred times. Mnt.Cost is set to 20. And E0 is set to 50. So, if net resource acquisition is 0, circles will die soon (about 3yrs after). For survival, the circle should be positioned in patches where offer at least 20 units of R every year. SD-of-d is set to 0.03. Therefore, the phenotypic variation (V_p) between parent and offspring is a maximum of 0.03. The results of the calibration are presented in the supplementary information comprehensively. The calibrated ranges of the primary parameters used in the simulation model are as follows. When parameters not listed in Table 3 are used in some simulation environment, they are described again.

Table 3 Main Parameter's value and Range

Parameter	Range	Parameter	Range
Int.No.	400	Mnt.Cost	20
E_0	0 ~ 100 (Mean 50)	Env.ht.	0 ~ 2
Max.R_0	0 ~ 300 (Mean 150)	M.E.R.	90 ~ 170
R.D.R. (M.R.D.R.)	0.30	SD-of-d	0.03
Mov.Cost	3 ~ 12	Age	15 ~ 40

3. Full Flowchart, Interface of the Model and Code of Programme

For convenience, the complete schedule of the model was included in the supplemental information. The model's display interface and full code are also presented

in the supplemental information.

Chapter 4. Results

The results are presented in two sections.

The first section presents the reliability and stability of the model and the results about the main research hypothesis related to niche specialization and frequency-dependent selection. Specifically, those are as follows. The second section presented the ecological factors affecting the fitness of agent with different d-values and the results about the evolutionary phenomena emerged with time in relation to the mismatch hypothesis. Specifically, those are as follows.

Section 1

Section 1 is presented in two parts as follows. Based on the order of model design, the results of reliability and stability are presented first. The results of the main hypothesis are then presented.

First, the model has trustworthy reliability and feasibility. TSS was varied according to their *d-value*. UA, NA and OA showed different TSS. The model provided stable ranges of *d-values* over time. And the proportions of UA, NA and OA were also stably different across the time. The simulation model showed stable and predictable results for 5 or 10 kyr. Stress tests were conducted for 97.5 kyr, and the stability of the model is confirmed.

Second, the model yielded the expected results of niche specialisation and frequency-dependent selection at least in the simulation environment. The population density was proportional to the local resource amounts. The local *d-values* were distributed differentially according to the amount of resources, and the numbers of UA, NA, and OA were distributed as expected with niche specialisation. The counts of UA, NA, and OA were negatively correlated with each other in the correlation analysis.

1. Reliability and Feasibility of the Model

1.1 Statistical Analysis of *d-value*, TFR, TSS and TT of UA, NA, OA

Within the primary calibrated model environment, descriptive statistical analysis was performed, and the summaries of them are presented in the table below. The analysis of variance (ANOVA) was performed on d, population, TSS, Total Energy, and TFR to see the differences between the groups (UA, NA and OA). Bartlett's test was performed, and each group was found to have the same variance. As will be explained later, the proportion of each subpopulation group was undoubtedly stabilised after about 0.5 to 1.5 kyr, even if an extreme initial condition is given. Therefore, data from 1,501 years to 5 kyr were collected and analysed. Most simulations were repeated for 16 times, that is 80 kyr.

Simulations were performed for 5 kyr. Several Mov.Cost and M.E.R. values were applied within the calibrated ranges. There were significant differences in d, population, TSS, total energy, age, and TFR between varied environmental conditions except for one condition. Also, there were significant differences among the three groups of UA, NA, and OA in the same environmental conditions (Table 2).

Especially TSS showed remarkable differences among the three subgroups (UA, NA and OA). In the environment where Mov.Cost is 7 and M.E.R. is 130, the TSS of UA was 0.2175 +/- 0.0621, but the TSS of NA was 0.4189 +/- 0.0750 and the TSS of OA was 0.8070 +/- 0.1794. In the environment where Mov.Cost is 7 and M.E.R. is 150, the TSS of UA was 0.2104 +/- 0.0559, but the TSS of NA was 0.4120 +/- 0.0586, and the TSS of OA was 0.7938 +/- 0.1638 (Table 2). This tendency suggests that the average TSS of the circle increases as Mov.Cost increases, and that the difference among the subgroups is maintained so that the sub-models of this simulation algorithm work well.

Table 3 The *d-value*, Populations, TSS, Energy, Age and TFR according to Mov.Cost and M.E.R.

Mov.Cost - M.E.R. (repetitions)		**3-130 (16)**	**7-130 (16)**	**12-130 (16)**	**F**
d-value	Mean	1.017	0.954	0.815	774.71*
	SD	0.037	0.034	0.030	
Population					
Total	Mean	736.3	641.7	560.5	286994.23*
	SD	29.6	26.2	20.6	
UA	Mean	149.1	169.1	345.6	451.81*
	SD	54.6	56.2	52.3	
NA	Mean	400.0	400.2	208.7	586.98*
	SD	60.1	54.0	51.1	
OA	Mean	187.2	72.4	6.2	543.29*
	SD	52.0	28.5	5.8	
F		625.73*	1498.44*	1882.26*	
TSS					
Total	Mean	0.2714	0.4115	0.4858	492.16*
	SD	0.0651	0.0810	0.0806	
UA	Mean	0.1089	0.2175	0.3773	6066.92*
	SD	0.0418	0.0621	0.0651	
NA	Mean	0.2260	0.4189	0.6363	7352.47*
	SD	0.0554	0.0750	0.0995	
OA	Mean	0.4899	0.8070	1.2647	2984.14*
	SD	0.1084	0.1794	0.6692	
F		5684.67*	7451.49*	5161.64*	
Total E.					
Total	Mean	314.88	316.81	300.09	266.90*
	SD	46.99	48.44	42.53	

UA	Mean	309.99	314.54	308.08	31.36*
	SD	94.42	92.57	55.92	
NA	Mean	314.44	322.08	290.05	773.12*
	SD	58.01	58.02	66.36	
OA	Mean	322.73	299.40	244.86	1070.44*
	SD	81.65	123.61	171.58	
F		96.72*	232.39*	880.26*	
Lifespan					
Total	Mean	29.62	28.08	26.24	13367.69*
	SD	1.85	1.69	1.36	
UA	Mean	29.29	27.65	26.27	5143.68*
	SD	3.68	3.17	1.75	
NA	Mean	29.50	28.27	26.24	5444.84*
	SD	2.27	2.05	2.29	
OA	Mean	30.32	28.34	26.19	1500.68*
	SD	3.36	4.95	7.32	
F		625.72*	156.64*	0.69	
TFR					
Total	Mean	1.009	1.008	1.004	1500.69*
	SD	0.158	0.162	0.157	
UA	Mean	0.991	0.993	1.004	31.91*
	SD	0.399	0.361	0.211	
NA	Mean	1.016	1.021	1.005	159.76*
	SD	0.217	0.207	0.259	
OA	Mean	1.000	0.958	0.866	361.12*
	SD	0.322	0.479	0.698	
F		102.72*	484.23*	560.90*	
Mov.Cost - M.E.R. (repetitions)		3-150 (16)	7-150 (16)	12-150 (16)	F
d-value	Mean	1.023	0.957	0.811	1727.05*

	SD	0.039	0.029	0.027	
Population					
Total	Mean	721.194	629.6	550.0	393212.31*
	SD	23.114	19.5	15.9	
UA	Mean	132.187	147.4	353.6	925.59*
	SD	54.386	50.3	47.9	
NA	Mean	407.822	420.3	192.9	1041.69*
	SD	52.928	50.6	47.8	
OA	Mean	181.185	61.9	3.5	1745.68*
	SD	52.275	22.4	3.9	
F		1808.12*	4537.68*	2250.05*	
TSS					
Total	Mean	0.269	0.4035	0.4690	811.18*
	SD	0.058	0.0632	0.0648	
UA	Mean	0.103	0.2104	0.3761	7904.55*
	SD	0.039	0.0559	0.0533	
NA	Mean	0.225	0.4120	0.6220	8427.23*
	SD	0.046	0.0586	0.0848	
OA	Mean	0.482	0.7938	1.2160	5198.41*
	SD	0.094	0.1638	0.7747	
F		20008.39*	12095.97*	7757.28*	
Total E.					
Total	Mean	360.926	366.06	352.11	179.30*
	SD	47.375	50.23	48.08	
UA	Mean	357.364	364.54	361.45	52.42*
	SD	109.72	107.35	61.94	
NA	Mean	361.047	370.56	337.44	977.92*
	SD	58.932	59.85	78.90	
OA	Mean	365.402	344.21	282.81	1031.37*
	SD	88.611	145.88	196.18	

F		63.73*	406.92*	1011.27*	
Lifespan					
Total	Mean	31.114	29.57	27.72	16465.67*
	SD	1.823	1.72	1.52	
UA	Mean	30.848	29.14	27.79	7827.94*
	SD	4.147	3.61	1.93	
NA	Mean	31.003	29.73	27.64	6919.09*
	SD	2.247	2.07	2.68	
OA	Mean	31.684	29.81	27.55	1253.79*
	SD	3.507	5.66	8.18	
F		429.39*	159.89*	5.24*	
TFR					
Total	Mean	1.005	1.005	1.002	53.44*
	SD	0.154	0.161	0.162	
UA	Mean	0.984	0.979	1.005	132.21*
	SD	0.424	0.383	0.212	
NA	Mean	1.014	1.020	1.000	162.95*
	SD	0.209	0.201	0.270	
OA	Mean	0.996	0.948	0.845	339.12*
	SD	0.326	0.512	0.716	
F		205.17*	440.96*	506.41*	

*p<.05.

1.2 The Time-Series Proportion of UA, NA and OA.

The simulation model worked reliably as the niche specialisation model. The relative proportions of UA, NA, and OA are shown in the following chart (Fig. 6). The simulations were repeated for a total of 80 times. There was a slight tremor of each proportion over time, but the proportion of UA and OA was relatively low compared to NA during the most period. UA variability was higher than that of OA, but it was increased

and decreased each other in an inverse way. After an average of about 400 yrs, the frequency of UA, NA, and OA entered a stable state and then continued consistently for 5 kyr.

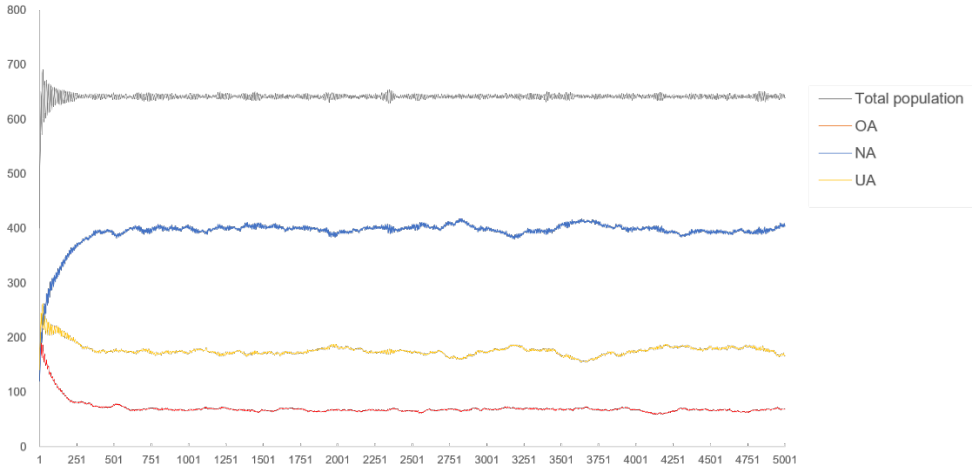

Figure 6 the Proportion of UA, NA and OA Over Time.

If a balancing selection by a niche specialisation occurs, a stable frequency will be reached even if the initial *d-value* of the object is extreme. In the basic simulation setup, the *d-value* was set to 0.5, 1.0, and 1.5, respectively, and randomly selected one of the three *d-values* in each circle. So, experiments were conducted to ascertain whether *d-value* converged to a similar value even if it started at 0.5 or 1.5. The experiments were repeated for a total of 32 times. If the initial *d-value* remains unchanged or does not converge to a particular level, the assumption of balancing selection model should be rejected in the simulation environment. However, despite the extreme initial setting, the *d-value* converged to constant value over time. This agent-based model of defence activation disorder shows the expected outcomes of balancing selection. The relative proportion of UA, NA and OA became stable after about 1 kyr (Fig. 7).

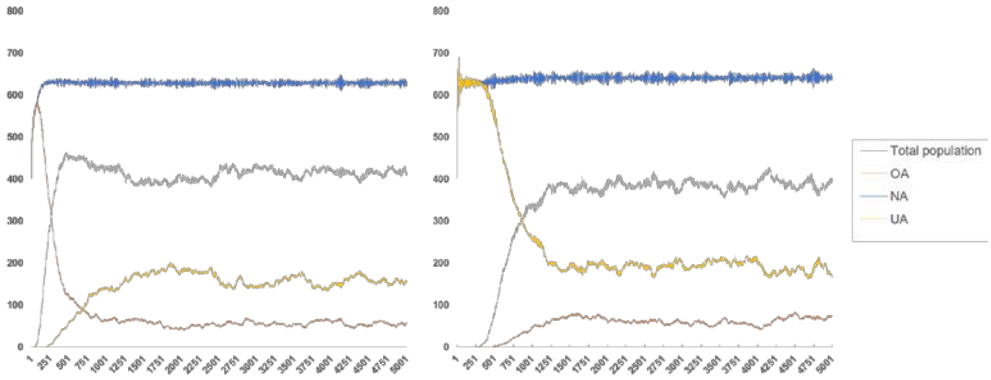

Figure 7 the Relative Proportion of UA, NA, and OA over time according to *d-value.*

Lt.: When the initial *d-value* is set to 1.5 (all objects are OA), the relative proportion of UA, NA, and OA over time. Rt.: When the initial *d-value* is set to 0.5 (all objects are UA), the relative proportion of UA, NA, and OA over time.

When *d-value* of each circle was randomly assigned from 0.5, 1.0, and 1.5 at the beginning, the standard deviation decreased gradually with time, and *d-value* converged to a value close to 1. The mean *d-value* was 0.949, and the standard deviation was 0.156. When *d-value* of each circle was fixedly assigned between 0.5 and 1.5 at the initial setting, the standard deviation gradually increased over time but stabilised at a similar level. And *d-value* also converged to a value close to 1 as well. The mean *d-value* was 0.939 and 0.947, and the standard deviation was 0.149 and 0.138, respectively. After about 1.5 kyr, they converged to similar patterns (Fig. 9).

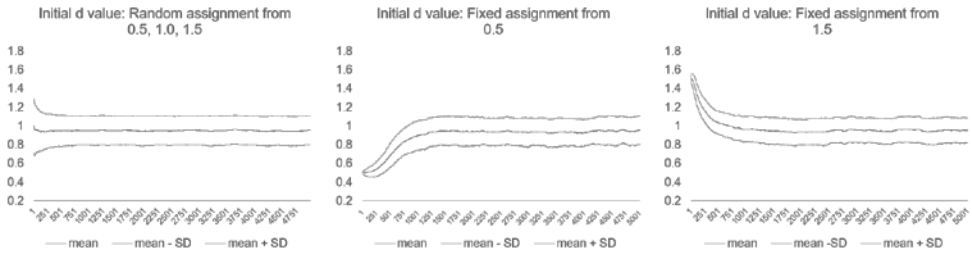

Figure 8 A Time-Series Pattern of *d-values* and SD-of-d under Three Different Initial

Settings.

As the above results, *d-value* of the circle stably converged in the simulation model. The initial condition affected the distribution, but after about 0.5 to 1.5 kyr, the influence of it disappeared.

Will this stable tendency persist for a very long time? The simulations were conducted under the same conditions for about 100 kyr (97.5 kyr). The results are shown in Fig. 9 (Note: Until 45 kyr, four runs were averaged, and then three runs were averaged). The average of *d-values* for the 97.5 kyr was 0.95374 +/− 0.018, and the maximum and minimum values were 1.016 and 0.895, respectively. Based on the above results, it is concluded that the agent-based simulation model of defence activation disorder has fine reliability and feasibility.

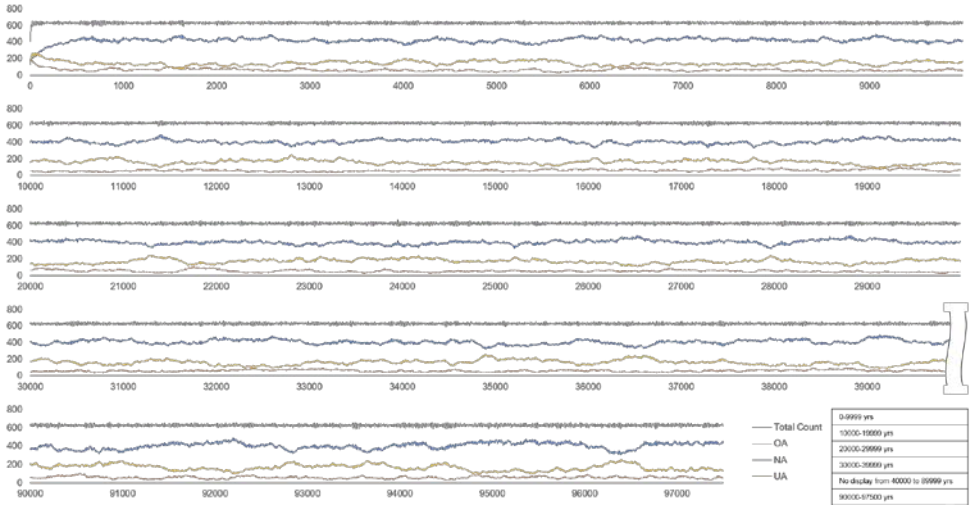

Figure 9 Changes in UA, NA, and OA fractions by 97.5 kyr.

2. Niche Specialization and Frequency-Dependent Selection

2.1 Geographical Localization of *d-values*

This simulation model was designed to distribute the resource amount in a direction on a two-dimensional continuous plane. In default mode, maximum R is 300, and the minimum R is 0. From 1501 to 5 kyr, data on the location and *d-value* of circles according to the resource distribution were collected and analysed. The optimal *d-value* of the individual differs according to the resource distribution. Also, the local population densities varied depending on the amount of resources. As Mov.Cost increased, circles tended to gather in places with many resources, but the overall distribution was similar. The absolute *d-value* was also different, but the tendency of the difference according to the resource gradient was somewhat identical (Fig. 10).

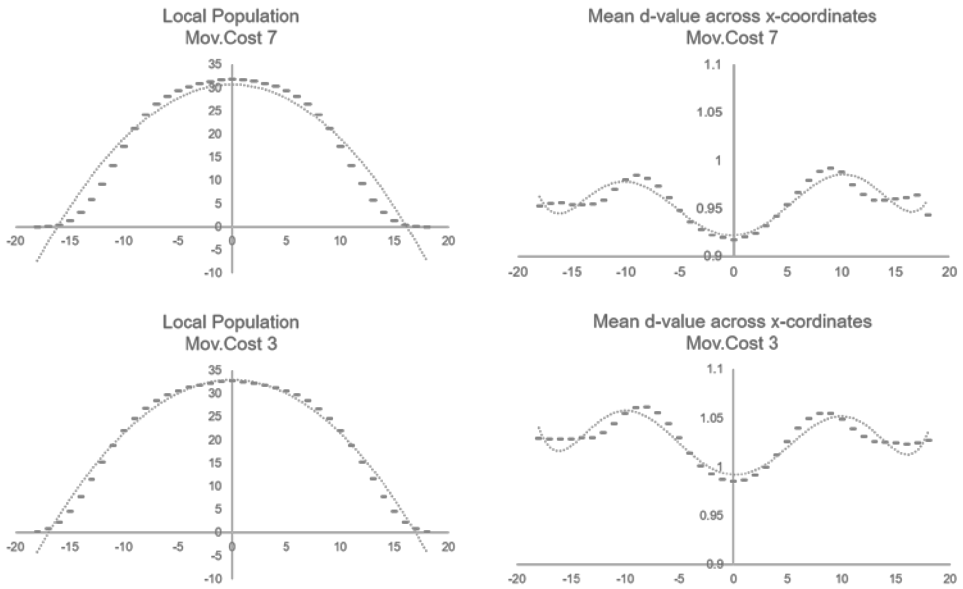

Figure 10 Distribution of local populations and the average *d-value* according to resource gradient of the x-axis (y-axis reflects the average population)

As commented in chapter 2, the circles of the simulation model have been simplified not to sense any information from patches or other circles without the R of the

current patches. There is no communication and no memory. However, over the generations, the circles were specialised for local niche's environment. The model shows the phenomenon of niche specialisation well.

On the contrary, when the resources are uniformly distributed in the whole environment, there is no local population difference (Fig. 11). In addition, no regional population differences were observed when the resources were randomly distributed unequally in the overall environment (Fig. 12). From these results, the null hypothesis can be rejected (Ch. 2).

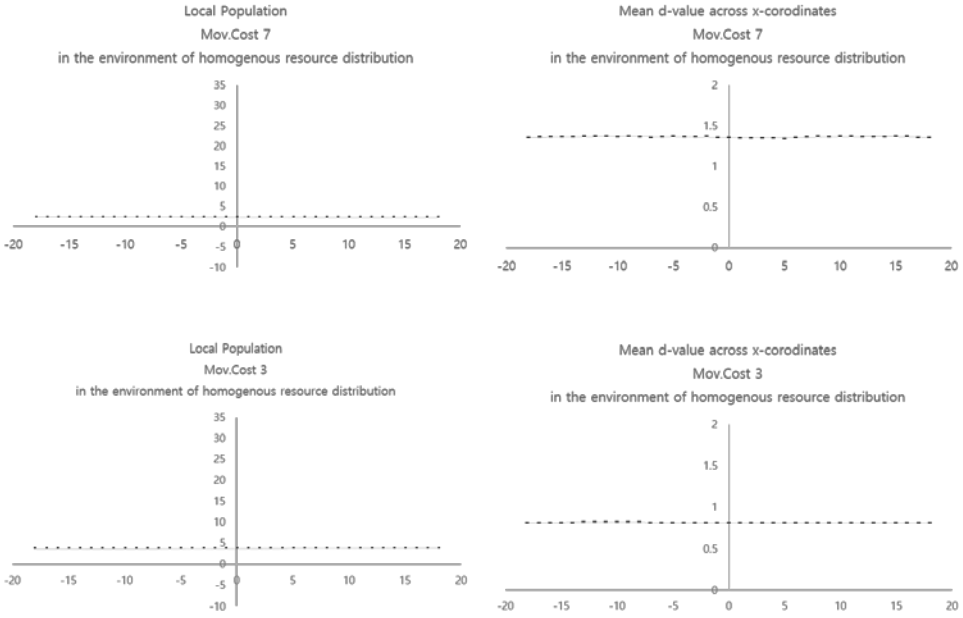

Figure 11 Distribution of local populations and the average *d-value* in the environment of homogenous resource distribution

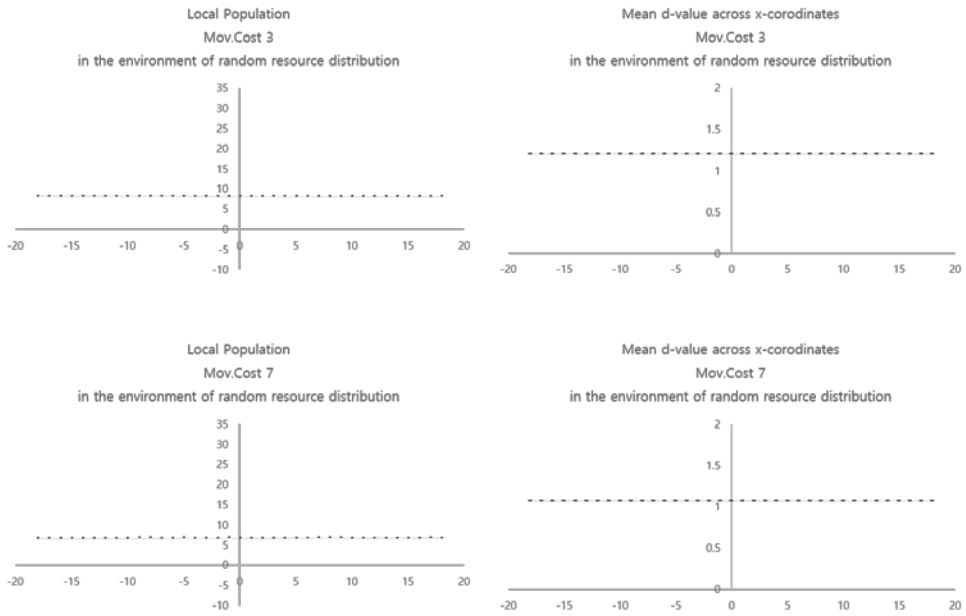

Figure 12 Distribution of local populations and the average *d-value* in the environment of random resource distribution

2.2 Geographical Localization of UA, NA and OA

As mentioned above, the population density varies according to the amount of local resources. The population density of UA, NA, and OA were different from the distribution pattern of total population density. As can be seen in Fig. 13, NA was more populated in areas with high resources. However, OA was relatively populated in areas with low resources. Of course, OA has also declined at patches where resources are scarce. In contrast, UA has a relatively high population in areas with high resources. The population declined rapidly in low-resource areas, but interestingly, UA had a higher population than OA in areas with very few resources.

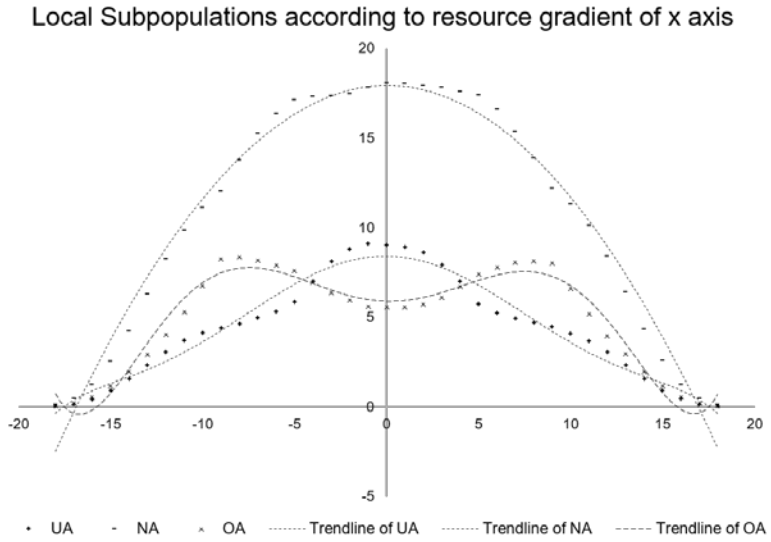

Figure 13 The population density of UA, NA, and OA according to resource gradient of the x-axis

Various optimal *d-values* are depending on each local environment. In other words, the diversity of defence activation level by niche specialisation was apparently observed in the simulation environment.

On the other hand, there was no difference in the local distribution of each subpopulation in the environment of homogenous or random resource distribution (Fig. 14). From these results, the null hypothesis can be rejected (Ch. 2).

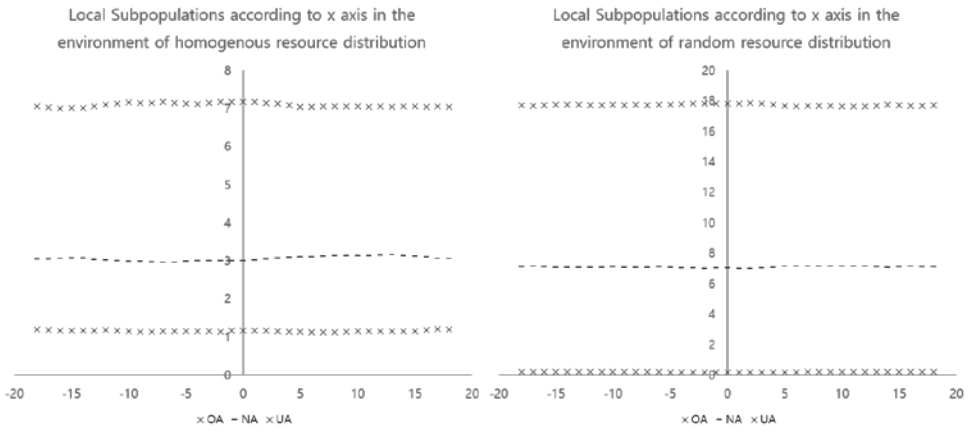

Figure 14 The population density of UA, NA, and OA in the environment of homogenous or random resource distribution

2.3 Correlation between each subpopulation

In an environment of Mov.Cost 7, the correlation of UA, NA, and OA population for 5 kyr was calculated (total 16 runs). NA and OA showed high negative correlations, and UA and OA also showed negative correlations. UA and NA also showed negative correlations, but the relationship was not robust when only the data after 1500 are considered (Fig. 15).

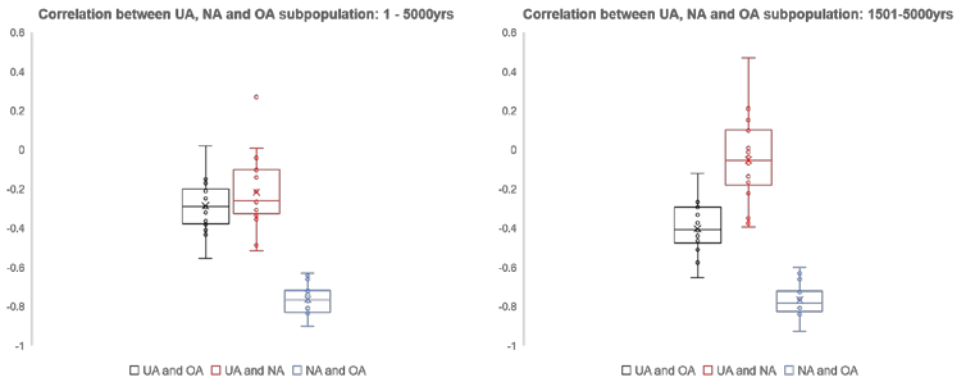

Figure 15 Correlation between the population of UA, NA, and OA.

In the simulation environments where the total population is limited, UA, NA, and OA showed inverse frequency-dependent selection. OA showed relatively high negative correlations with UA and NA. OA tends to have relatively high densities in areas with low resources. However, as the population of UA or NA increased, the number of patches optimised for OA decreased, because UA and NA moved to other areas more often. Over time, an OA or UA that has moved to a patch with a low resource will be unfavourable to OA because they have relatively suboptimal behavioural strategies.

In other words, in patchy environments in which the movement is not strictly restricted, and the amount of resources is graded, the populations of individuals with various *d-values* would maintain inverse frequency-dependent selection. The implications of this phenomenon are discussed later.

Section 2

Section 2 is presented in two parts as follows. First, the influence of three major factors (Mov.Cost, M.E.R., Max.D. and Env.Ht.) affecting *d-value* and the fitness of UA, OA and NA was established. First, the increase in Mov.Cost lowered the global average *d-value* and raised the proportion of UA. Interestingly, high Mov.Cost tended to increase UA population and UA's TFR variance. Second, as M.E.R. increased, *d-value*'s distribution tended to converge to one particular optimal value, and the whole population declined, but OA tended to be more vulnerable. Third, as Max.D. increased, *d-value* increased. In other words, as the fluidity increased, UA was more vulnerable.

Second, the changes in the overall *d-value* and changes in the subpopulations of UA, NA, and OA when the values of Mov.Cost and M.E.R. change with time is evaluated. The results were not different from the expectations. It took several hundred years to find a new steady state. During the period, the fitness of the individuals with the previous

optimal *d-value* fell.

1. Ecological Factors affecting the Fitness of UA, NA and OA

1.1 The effect of Mov.Cost on UA, NA and OA

In this simulation, Mov.Cost refers to the amount of E consumed when leaving to other ecological patches. Mov.Cost is the critical factor affecting fitness because E must cover the costs of survival and reproduction. If circles use too much Mov.Cost, it becomes difficult to survive or breed. Within the calibrated ranges, the total population decreased when Mov.Cost increased (Table 3). In the case of Mov.Cost 3, 7, and 12 (and M.E.R. is 130), the average population was 736.3, 641.7, and 560.5, respectively. There were significant differences in the population of subgroups between each condition. The percentages of UA, NA, and OA subgroups in each environmental condition are shown in Table 3.

When Mov.Cost was low, the population of OA has increased significantly. OA showed optimal behaviour where resources were scarce. However, since there were limited resources, absolute resource acquisition was relatively small. As Mov.Cost increased the population decreased rapidly compared to other subgroups because the energy obtained was less likely to reach M.E.R. When Mov.Cost was 3 and M.E.R. was 130, the population of OA was 187.2. When Mov.Cost was 12, the population of OA decreased to 6.2.

Conversely, when Mov.Cost was high, the proportion of UA has increased relatively. UA shows optimal behaviour at high resource levels. Therefore, it generally showed higher fitness than OA. The upsurge in Mov.Cost decreased the absolute fitness of UA, but in the environment where the population of the entire habitat was kept within constant ranges according to the logistic function, UA can enjoy the relatively better fitness, interestingly. If Mov.Cost was 3 and M.E.R. was 130, the population of UA was

149.1. If Mov.Cost was 12, it was increased to 345.6.

When Mov.Cost was high, the average *d-value* of the entire population tended to fall. When Mov.Cost was 3, the *d-value* was 1.017 +/- 0.037. When Mov.Cost was 7 and 12 (M.E.R. 130), the *d-values* were 0.954 +/- 0.034 and 0.815 +/- 0.03, respectively. This phenomenon is because a circle with relatively low *d-value* is advantageous in the environment with high Mov.Cost (Fig. 16, 17). For the same reason, *d-value* did not always converge to exactly 1. This tendency continued for at least 5 kyr (Fig. 18).

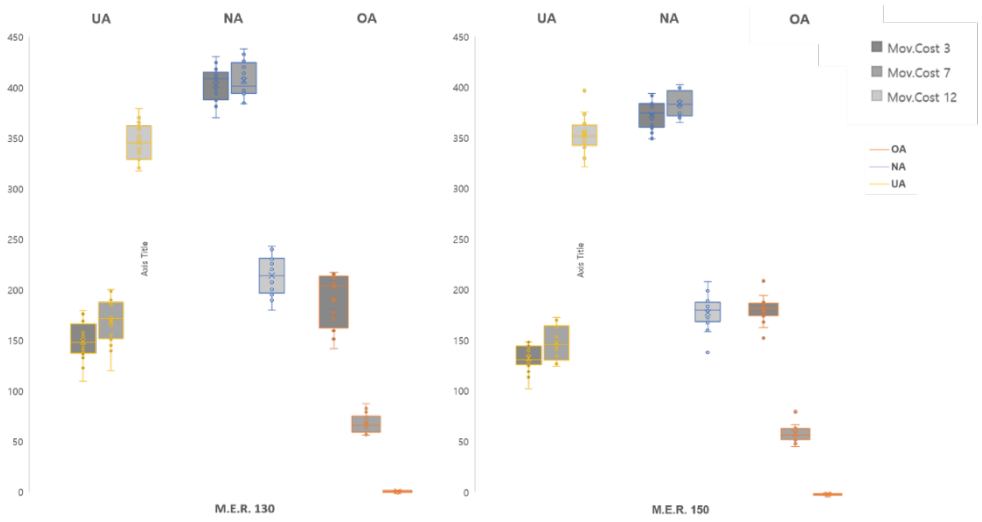

Figure 16 Population of Each Subgroup according to Mov.Cost. (M.E.R. 130)

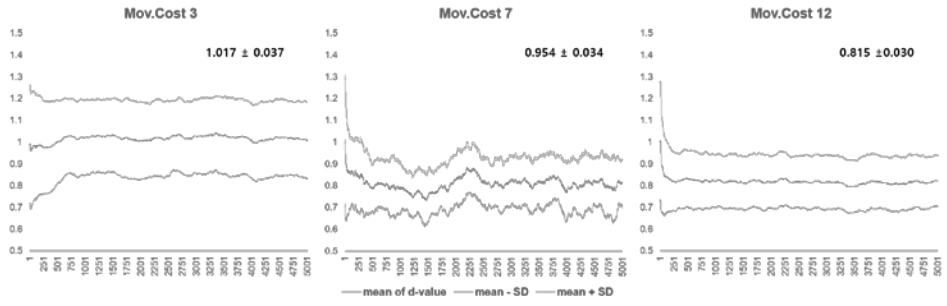

Figure 17 Time-Series Patterns of *d-value* according to Mov.Cost 3, 7 and 12 (M.E.R.130)

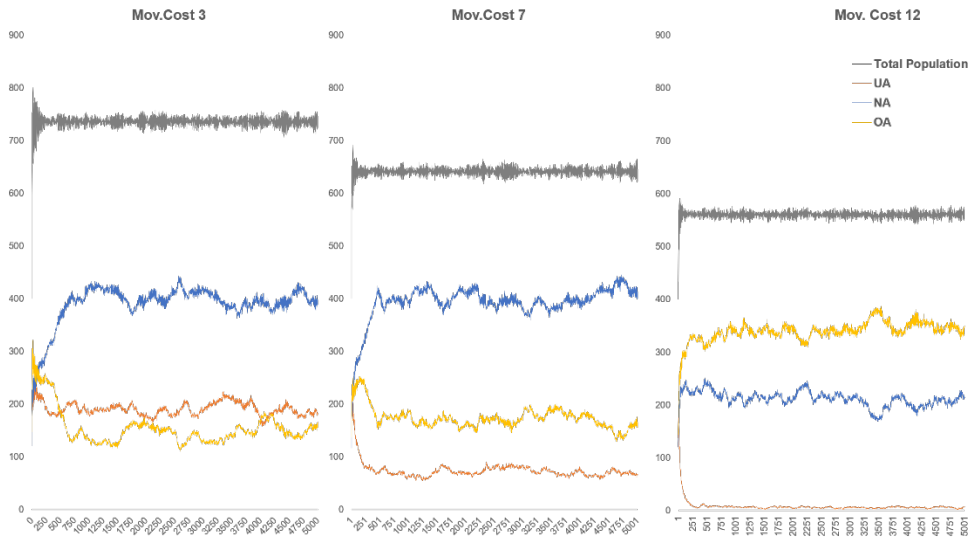

Figure 18 Time-Series Patterns of Sub-population UA, NA and OA (M.E.R.130)

There was a significant difference in the TFR of each subgroup. The TFR of NA (1.016 +/- 0.217) was the highest, regardless of environmental conditions (Table 2). When Mov.Cost becomes high, the reproductive fitness of OA seems to be relatively lower (0.866 +/- 0.698), and the reproductive fitness of UA seems to be relatively higher (1.004 +/- 0.211). For more accurate visualization, the simulation of 5 kyr for three environmental conditions was repeated 16 times, and the TFR data for a total of 240 kyr was obtained. Similarly, when Mov.Cost was high, the variance of the reproductive fitness of UA was relatively high, and vice versa (Fig. 19).

The decline in reproductive fitness is presumed to be due to the difference in the amount of energy obtained in each subgroup. In the environment of high Mov.Cost, the energy gain of the circle with high *d-value* decreased, and the variance of energy acquisition increased due to the high mortality. The differences in mortality rate, i.e., the

difference in lifespan, is described below.

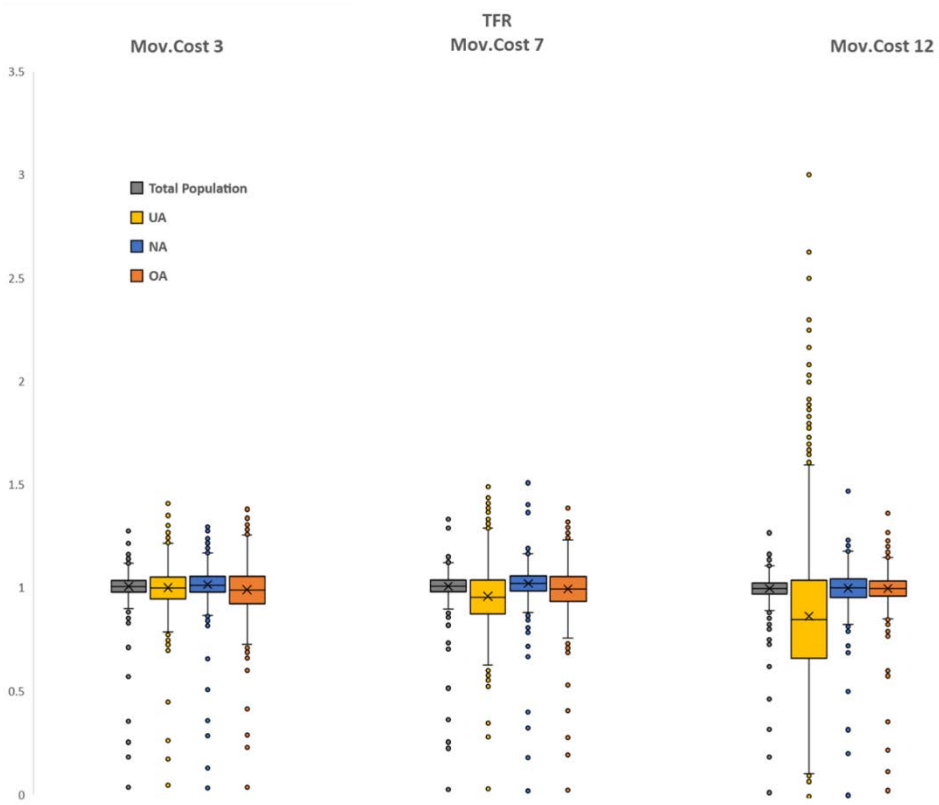

Figure 19 Comparison of the TFR of three Subgroups for a Total of 240 kyr

When Mov.Cost was higher, the lifespan was shorter relatively. When Mov.Cost was 3, the lifespan was 29.62 +/- 1.85. But the lifespan was 28.08 +/- 1.69 and 26.24 +/- 1.36, when Mov.Cost was 7 and 12, respectively (Table 3). Under the same environmental conditions, lifespan did not show remarkable differences among UA, NA and OA, despite statistical significance. However, as Mov.Cost increased, the variance of OA lifespan increased, while the lifespan of UA tended to converge to the average. These findings mean the environment with high Mov.Cost become more unfavorable to OA than UA.

1.2 The effect of Max.D. on UA, NA and OA

It was analysed how the distance that circles can move at one time, i.e. Max.D. affects the relative proportion of UA, NA and OA, and *d-value*. In the default model, an agent can move to one of the nearby eight patches. To verify the effect of Max.D., it was divided into 1, 2, and 3 according to the maximum radius from the current position. So, the number of possible patches an agent can move at a time is increased to 4, 12, and 28, respectively. The results are shown in Fig. 20 (8 runs for each situation).

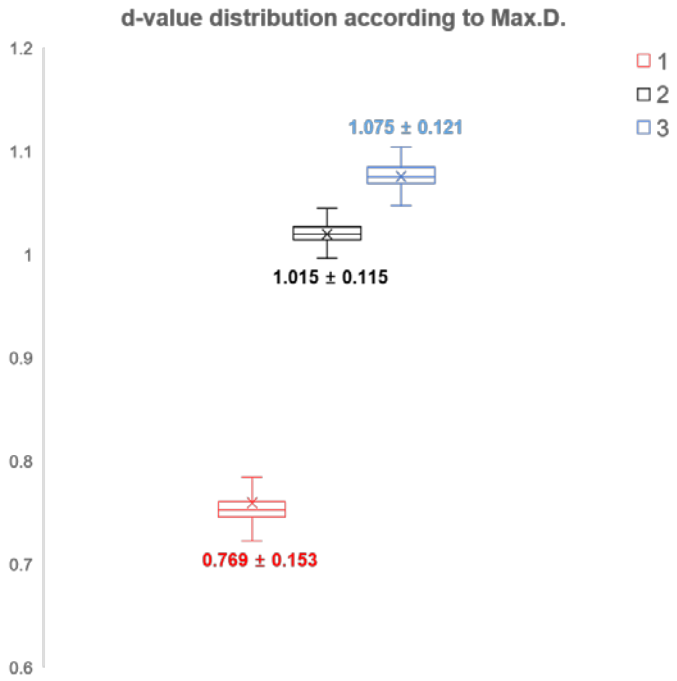

Figure 20 Relationship between *d-value* and Max.D

Interestingly, as the number of available patches increased, the overall *d-value* increased. When Max.D. was 1, *d-value* was 0.769 +/- 0.153 (Fig. 20). However, when

Max.D. was 2 or 3, *d-values* were 1.015 +/- 0.115 and 1.075 +/- 0.121, respectively (Fig. 20). Therefore, the proportion of UA decreased, and the ratio of OA increased, probably, due to the increased likelihood of UA moving to relatively unfavourable patches due to increased fluidity. On the other hand, for OA, if the Max.D. value rises, the possibility of moving to an unfavourable patch becomes lower than that of UA, relatively (Fig. 21). In other words, the increased socio-ecological fluidity could give relatively higher fitness to highly defensive individuals in the simulated environment.

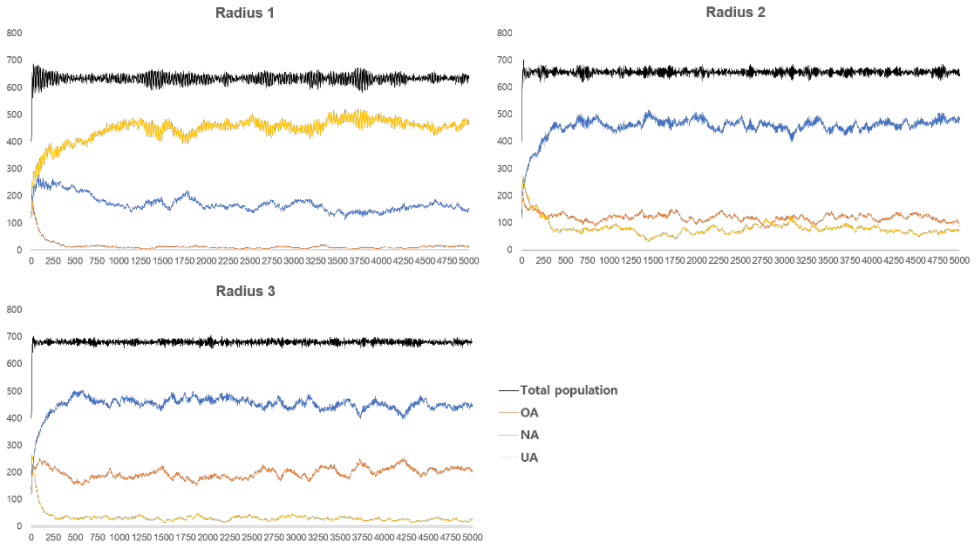

Figure 21 Proportion of UA, NA, and OA relative to Max. D.

1.3 The effect of M.E.R. on UA, NA and OA

When M.E.R. was increased by 20 units from 90 to 170, the change in population was simulated. The increase in M.E.R. appeared as declines in population. The total population decreased modestly from 675.12 +/- 7.96 to 629.44 +/- 4.94. UA, however, was the most frequent at M.E.R. 110 to 130 and fell in M.E.R. 150 (Table 4). On the other hand, the proportion of NA was not significantly changed. In the case of OA, as M.E.R. increased, the population decreased consistently. As M.E.R. increased, the overall *d-*

value tended to converge to the optimal *d-value*. However, the distribution of each subgroup maintained a similar pattern (Fig. 22).

An increase in M.E.R. resulted in an overall increase in lifespan. The average lifespan of at 90 units of M.E.R. was 24.61 +/- 0.25 but increased to 31.01 +/- 0.46 at 170 units of M.E.R. (Table 4), presumably, because it took more time to obtain the energy needed for reproduction.

Table 4 Changes in *d-value*, Population, and Age with Increasing M.E.R.

Mov.Cost - M.E.R. (repetitions)		7-90 (16)	7-110 (16)	7-130 (16)	7-150 (16)	7-170 (16)
d-value	Mean	0.986	0.960	0.951	0.955	0.956
	SD	0.154	0.153	0.145	0.137	0.133
Population						
Total	Mean	675.12	657.34	641.74	629.44	616.44
	SD	7.96	8.12	6.80	4.94	4.29
UA	Mean	145.09	172.44	170.54	153.40	145.14
	SD	17.29	14.49	15.76	12.97	10.05
NA	Mean	414.58	399.06	403.87	414.36	414.57
	SD	13.84	13.79	15.55	13.76	10.58
OA	Mean	115.45	85.84	67.33	61.67	56.74
`	SD	12.15	9.74	6.94	5.50	5.47
Lifespan						
Total	Mean	24.61	26.43	28.10	29.58	31.01
	SD	0.25	0.37	0.44	0.44	0.46
UA	Mean	24.05	26.02	27.68	29.16	30.61
	SD	0.62	0.70	0.81	0.91	0.99
NA	Mean	24.75	26.60	28.29	29.74	31.14
	SD	0.34	0.47	0.52	0.53	0.56
OA	Mean	25.05	26.80	28.38	29.83	31.36
	SD	0.74	1.08	1.38	1.50	1.63

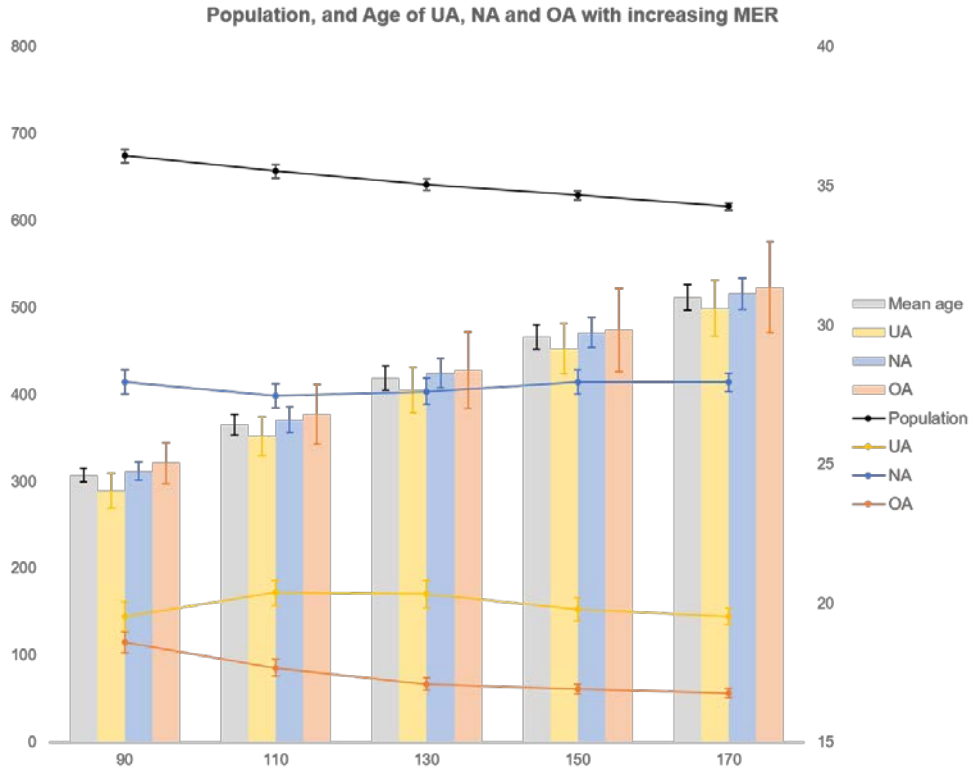

Figure 22 Population and Age of UA, NA and OA with increasing M.E.R.

The increase in M.E.R. in this simulation has made breeding or nurturing difficult and has the effect of limiting population growth. The rise in M.E.R. appears to have a more negative impact on OA than UA or NA (Fig. 22).

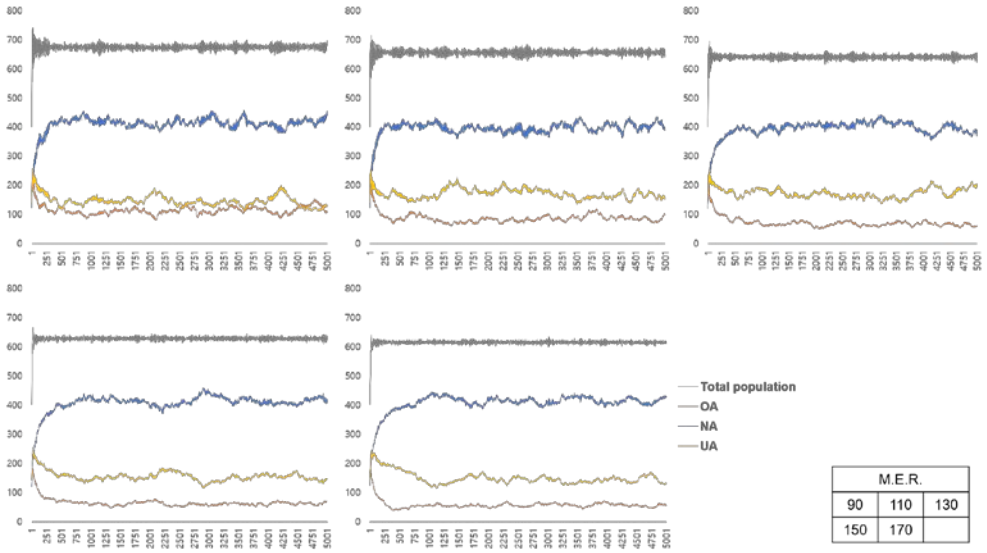

Figure 23 Time-Series Change of UA, NA, OA when M.E.R. is 90, 110, 130, 150, 170

1.4 The effect of Env.Ht. on UA, NA and OA

According to Env.Ht. (0.5, 1 and 1.5), the relative proportion of UA, NA, and OA was analysed. The average d values were 1.059 +/- 0.124, 0.948 +/- 0.163 and 0.857 +/- 0.183, respectively (Fig. 24). When the heterogeneity was low, the overall *d-value* tended to be high. Therefore, the proportion of OA increased, presumably, because UA, which frequently moves to new patches, become relatively under unfavourable situations. When Env.Ht. became higher, the overall *d-value* become lower. Therefore, the proportion of UA increased because the number of patches that are favourable to UA increased. OA is relatively advantageous at patches with low resource volumes, but it is nevertheless difficult to obtain M.E.R. where the resource is too low. So, too many patches with poor resources are also undesirable for OA.

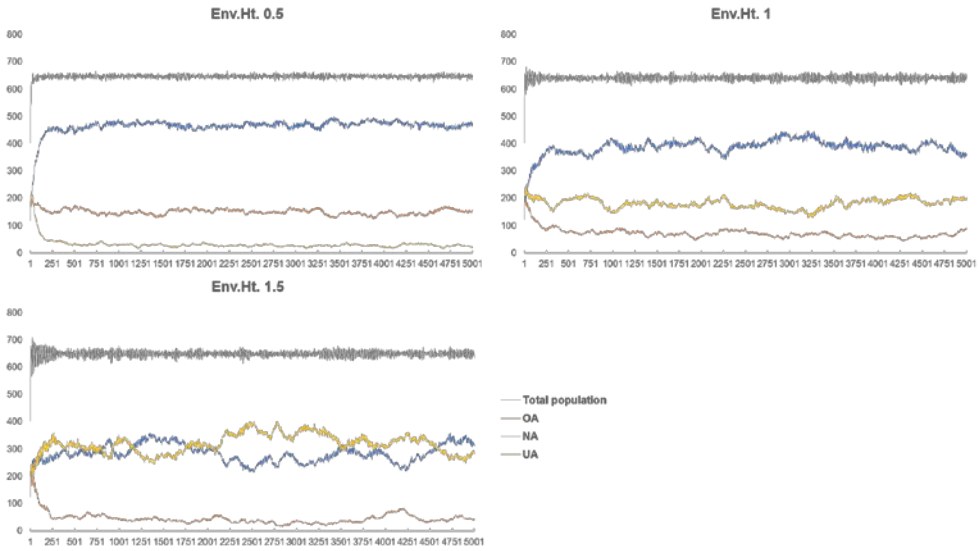

Figure 24 Proportion of UA, NA and OA according to Env.Ht.

2. Temporal Changes and Mismatch Phenomena

2.1 Temporal changes of Mov.Cost

As the simulation progressed for 10,000 years, Mov.Cost was changed 4 times (16 runs). In 2 kyr, Mov.Cost declined until 4 kyr. Mov.Cost increased in 6 kyr and lasted until 8 kyr. In 8 kyr, Mov.Cost went back. It took about a few hundred yrs to a thousand yrs to take a new equilibrium (Fig. 25). The decrease in Mov.Cost increased the average d value, and vice versa. A drop in Mov.Cost was disadvantageous to UA, and a rise in Mov.Cost was disadvantageous to OA. These patterns continued for many decades of generation.

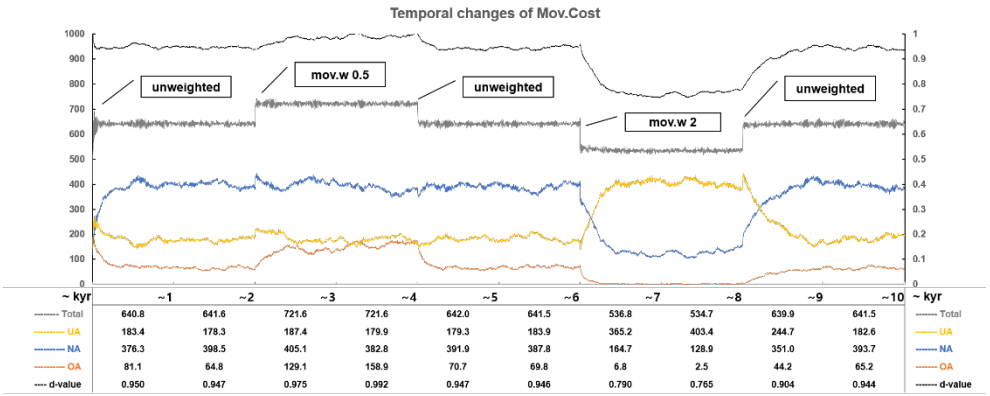

Figure 25 Change of *d-value* and the Proportion of UA, NA and OA according to the Temporal Change of Mov.Cost.

2.2 Temporal changes of M.E.R.

As the simulation progressed for 10,000 years, M.E.R. was changed 4 times (16 runs). In 2 kyr, M.E.R. dropped until 4 kyr. M.E.R. And M.E.R. raised in 6 kyr and lasted until 8 kyr. It took about a few hundred years to take a new equilibrium (Fig. 26). The decrease in M.E.R. increased the average d value, and vice versa. A drop in M.E.R. was disadvantageous to UA, and a rise in M.E.R. was disadvantageous to OA. However, the effect was small compared to the change of Mov.Cost.

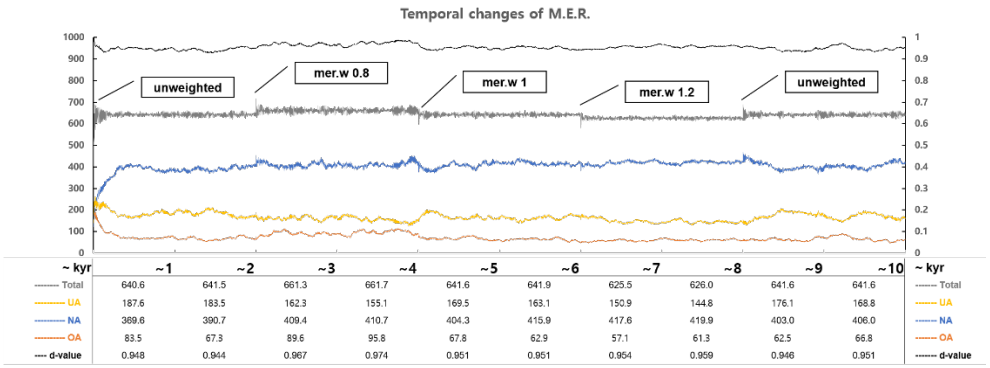

Figure 26 Change of *d-value* and the proportion of UA, NA and OA according to

temporal change of M.E.R.

Chapter 5. Discussion

1. Feasibility of Agent-Based Evolutionary Simulation Model of D-type Disorder

This study is compatible with previous researches that adaptation in localised areas can evolve various behavioural patterns (Bergmüller and Taborsky 2007; Montiglio, et al. 2013a). Moreover, the results also show that defence activation can be maintained as ESS at different levels in the simulation environment by balancing selection. Niche specialisation is a potent hypothesis explaining why there are various behavioural patterns (Futuyma 2013). Agent-based Evolutionary Simulation model of D-type disorder is one useful way to see how niche specialisation occurs and what the environmental requirements for it are.

Beside balancing selection model, several potential evolutionary explanations have been proposed for the ultimate causations of dysfunctional behavioural patterns (Park 2019b; Park 2019c). Most of them are explained in the introduction briefly. Why are so many hypotheses struggling with each other until now? There may be two reasons. First, the conceptual pluralism may reflect the complex nature of the psychological disorder (Parijs 1981). Since the human mind is so complex, there have been many hypotheses about it so far. It must of necessity be so. Second, it may reflect the diverse academic interests and historical traditions about the human mind. Competing hypotheses are featured by a lack of theoretical agreement and many models are vigorously conflicting with each other (Cartwright 2008). A theoretical framework that can encompass many phenomena will be a solid background for building a general theory of human behaviour {Muthukrishna, 2019 #2027}.

For an empirical evolutionary study of dysfunctional behavioural patterns, some problems must be solved (Park 2019a). First, proxy indicators as an interim measure

should be established for the evolutionary study of human psychological phenomena. It is because the human mind is too complex to be quantified objectively (Comer 2010). Therefore, a human behavioural ecological approach can be useful. A simple and straightforward approach is needed. Second, appropriate currencies should be presupposed as proxy indicators. It should be universal, measurable, simulatable, and directly connected to fitness. Third, appropriate research methods are needed to observe how dysfunctional human behaviour evolved in the scale of geological time. The human mind does not remain in the fossil. Studies about contemporary hunter-gatherer studies have a variety of limitations, including small populations and external effects due to globalisation. Most of all, hunter-gatherers are not primitive survivors. Archaeological research could be useful for studying the evolution of general human psyche, but not for studying dysfunctional behavioural patterns (Park and Pak 2015).

To set the interim model, in this study, the agent-based model quantified the psychological state of anxiety, depression, and obsession as energy acquisition using the MVT. Although psychological mechanisms have not evolved solely to activate defence modules, in this study, we proposed the MVT model that can quantify defence activation level by correlating them to the appraisal weight (i.e., *d-value*) for the ego, the world and the future. There has been no study that have quantified the traits of dysfunctional behavioural patterns in the context of human behavioural ecology or evolutionary neuro-anthropology as far as I know.

MVT is a well-established ecological theorem and has already proven its value in explaining animal and human migration phenomena (Charnov 1976). Animal studies have already been conducted using simulation models using MVT (Wajnberg, et al. 2000), and the theorem is useful for explaining the mobility of foraging society (Kelly 2015). However, a simulation model of depressive disorder or anxiety disorder using MVT has not been proposed.

Of course, although MVT is a compelling ecological model, it is not possible to explain all features of the dysfunctional behavioural patterns of human with MVT.

Nonetheless, simplified models can be useful in explaining aspects of complex human behaviours and evolutionary phenomena. It is not necessary to say again that the most critical element in the agent-based model is simplification (Railsback 2012). In this paper, the effect of defence activation level, i.e., *d-value*, on ecological currency, i.e., the acquisition of energy, was studied.

In this model, the city is used in three life activities, i.e., the movement cost, the maintenance cost, and the reproductive cost. As a result, the reproductive fitness of each can be calculated. Using ABM, it is elucidated for what evolutionary phenomena emerge in the geological timescales. As a result, this simulation model has proven to be an effective and straightforward method for evolutionary analysis of defensive activation disorders. Perhaps the results of the model can be applied to infer the phenomena of the real world.

2. Niche Specialisation and Frequency-Dependent Selection

According to the results of the study, each individual was adapted to have optimal *d-value* corresponding to local environmental conditions. The local optimal *d-value* was different from the global optimal *d-value* of the entire habitat. It was also observed that individuals with different *d-values* clustered differently depending on the local environment. In the resource-rich area, the subgroup with low defence activation level was clustered. In contrast, in resource-poor area, the subgroup with high defence activation level was clustered. The model showed that multiple defence activations level could be ESS by the mechanism of balancing selection, specifically, niche specialization, at least, in a simulated environment. A schematic diagram is shown below (Fig. 27).

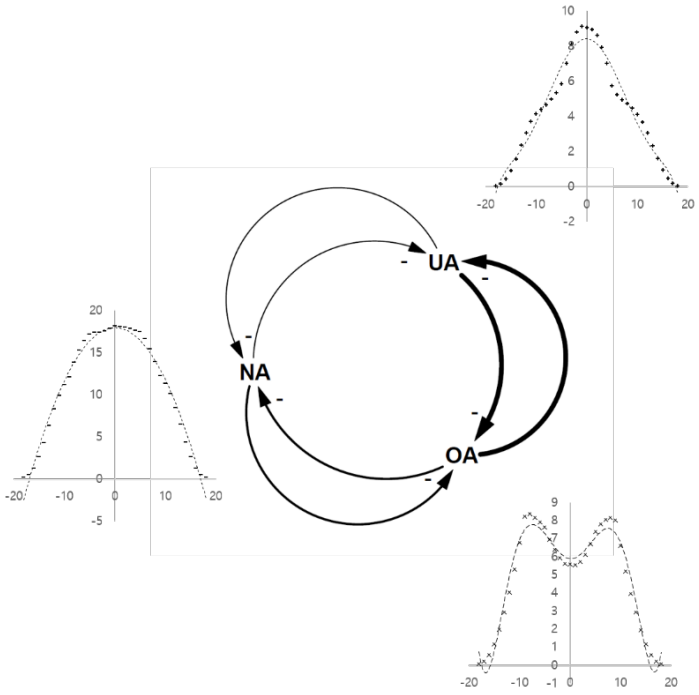

Figure 27 Niche Specialization and Frequency-Dependent Selection of UA, NA and OA

However, this phenomenon did not occur when resources were randomly distributed (not shown in this study). The random patchy environment was a prerequisite for ensuring the universality of all individuals with a global optimal *d-value*. If all other factors are controlled, different levels of defensive behaviour are less likely to be evolved. The Total Niche Width (TNW) of the population can be divided into the Within-Individual Component (WIC) and Between-Individual Component (BIC) (Bolnick, et al. 2010). All individuals in this model were premised to have the same mental and physical abilities. So Env.Ht. affect the BIC and *d-value* is only WIC. Specialisation occurs when WIC are much smaller than TNW or BIC is a large proportion of TNW. Therefore, under the evenly patchy environment, specialisation is hard to occur because BIC is small. However,

under the resource-gradient environment, specialisation can occur quickly if free movement is limited.

In this study, the amount of resources that each individual expects depends on the resource of birthplace. Much of TNW is BIC. In the real world, however, the differences in individuals are significant. In future studies, it is necessary to investigate whether and how WIC, that is, individual traits influence the specialisation.

Also, as the population of a subgroup increased, the number of other subgroups increased. If a balancing selection occurs only by a niche specification, the fluctuation of the proportion of individuals with different *d-values* will be minimised. This is because the total number of niches is limited. Since the number of niches where their d value is optimal is limited, the growth of the sub-population increases the likelihood of moving to the suboptimal area. Thus, the niche specialisation phenomenon could work as the environmental factor that maintains the proportion of subgroups with different d values in a frequency-dependent manner (Bergmüller and Taborsky 2007). However, it does not appear as a predator-prey relationship, as the Lotka-Volterra equation (Brauer, et al. 2001) suggests. It is unclear what the negative correlation in this study has evolutionary meaning. A more sophisticated model is needed to distinguish the effects of the niche specialisation and frequency-dependent selection.

In conclusion, the simulation results offer theoretical support for the argument that defence activation levels can be maintained by multiple-niche polymorphism. The *d-value* by itself does not induce absolute selection pressures, but a variety of optimal *d-values* may appear over the long term through relative superior fitness to others in various microenvironments (Futuyma 2013). The multiple-niche polymorphism model could work with multiple ESS if the geographic or social gradient of the environment does not change often.

3. Mobility

In this paper, mobility is divided into two parts. First, mobility is related to the cost of moving once. In this model, all individual can only move to the surrounding patches. Therefore, the movement cost acts as a geo-ecological limiting factor. Second, mobility is related to the maximum distance an individual can move at a time. Therefore, the fluidity could act as a socio-ecological limiting factor, so-called social mobility (Heckman and Mosso 2014). As movement costs increased, the fitness of individuals with a highly activated defence has decreased. Also, as fluidity increases, the fitness of individuals with a highly activated defence has increased. A schematic diagram is shown below (Fig. 28)

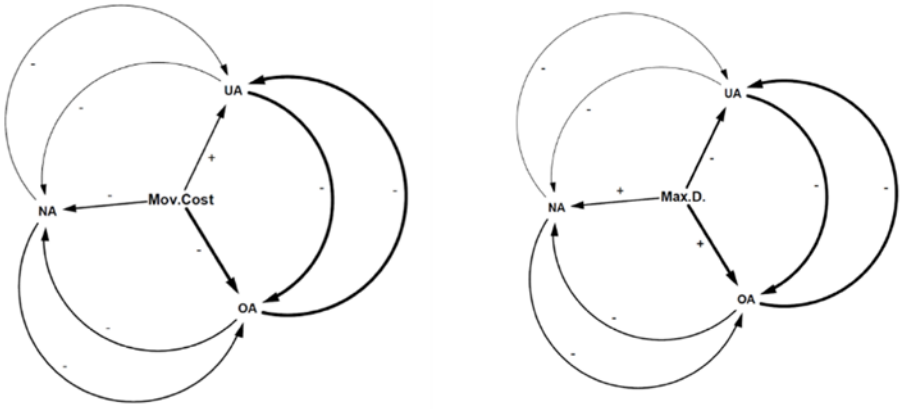

Figure 28 Effect of Mobility (Mov.Cost and Max.D.) on UA, NA and OA

Mobility is the oldest tradition of humankind. The hunter-gatherer has continued to change residence. The sedentary lifestyle is a relatively recent form of life. The hunter-gatherer is sometimes defined as people who “move around a lot” (DeVore and Lee 1968). Adaptation to the environment has played a significant role in the diversity seen in hunting and gathering societies (Kelly 2015). After the Younger Dryers, geographical and environmental heterogeneity has been decreased because people began to settle

in the same ecological environment. However, social heterogeneity has been increased because differences in the social-ecological environment have begun to emerge.

The results showed that the increase of movement cost or decrease of fluidity has the same effect. Perhaps the selective pressure of geographical mobility in hunter-gathering societies may be similar to the selective pressure of social mobility of stratified societies. Even though human adopted the sedentary lifestyle for a long ago, environmental heterogeneity has been switched with social heterogeneity. In a sense, humans are still moving around. Humans are changing jobs, moving to distant cities, migrating to other societies, making new families, getting higher social status, or losing his or her social status.

The relationship between social mobility and depressive disorder is well known. However, most studies are on the relationship between downward social mobility and depressive disorders (Nicklett and Burgard 2009; Tiikkaja, et al. 2013). Upward social mobility has been studied as generally providing mental health benefits (Chan 2018).

There is, of course, a minority opinion that social mobility has nothing to do with depressive disorder (Hoven, et al. 2019). However, these studies mainly deal with the psychological response of individuals as they experience social mobility. From an evolutionary point of view, the increase in social mobility leads to large-scale changes in ecological conditions. The reduction of mobility lowers the fitness of individuals with high activated defence module, which has been locally optimal to some resource-poor niches. According to the mismatch hypothesis, some neutral traits could be converted to negative traits under the radical changes in environmental conditions. Therefore, the results of this study may explain the central paradox of defence activation disorder, at least, in the simulated environment.

4. Reproductive cost

As the reproductive cost increased, the total population decreased. The average

lifespan of the population also increased. With increasing reproductive costs, individuals with higher levels of defence activation showed higher vulnerability. However, when the reproductive cost increased very much, the fitness of individuals with low defence activation level also decreased. The increase in reproductive costs has resulted in a relative increase in the fitness of individuals with optimal behaviour strategies at the overall habitat level. A schematic diagram is shown below (Fig. 29).

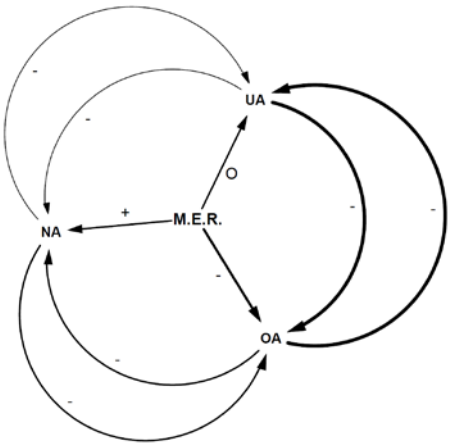

Figure 29 Effect of Reproductive Cost on UA, NA and OA

The reproductive cost in this study include the costs of pregnancy and childbirth and the costs of nurturing. Compared to the hunter-gathering society, the TFR has increased considerably in the agricultural society (Zihlman 1982). In the hunting society, the average number of offspring was five, but in agricultural societies, the number of offspring increased to ten (Cartwright 2016). Perhaps it is because the direct reproductive cost was decreased due to group parenting, reduced need for mobility, and the availability of substitute mother (Gibson and Mace 2005; Trevathan 2010). In addition, since the lactating period was long in the hunting gathering society, the fertility rate may be low due to lactational amenorrhea {Trevathan, 2010 #1971}. However, the fertility rate has been declining recently, especially in health-rich countries. The TFR is only about

two (Alkema, et al. 2011). There are various arguments as to why the fertility rate declines in industrial countries (Kaplan, et al. 1995). For example, investment such as schooling or training for offspring has increased (Kaplan and Lancaster 2000). The help of the alloparents such as grandparents have also decreased (Turke 1989).

When the reproductive cost increases, it become hard to breed in the resource-poor area for an individual with low *d-value*. Even though behavioural strategy based on low *d-value* is the locally optimal strategy on poor area, it becomes too hard to get minimal energy for reproduction. So, increased reproductive cost leads to a more rapid decline in the fitness of individuals exhibiting defensive activation disorders.

When the reproductive cost was increased too much, the fitness of individuals with low d values also decreased. The standard deviation of the *d-values* of the whole population was reduced. In other words, the reduction of population occurred mainly in the subgroups with high or low *d-value* (D-type disorder or d-type disorder).

The increase in reproductive costs may be advantageous for individuals who exhibit optimal behavioural strategy in terms of overall habitat. More sophisticated research is needed, taking into account the ratio of total resources to breeding cost, but this is an interesting finding. Decreased cost of reproduction after the Neolithic revolution may have increased the frequency of individuals with suboptimal *d-values*. In modern society, the soaring breeding cost may be lowering the fitness of individuals at the extremes. This may be the alternative scenario to explain the evolutionary paradox of defence activation disorders in the simulated world.

5. Environmental Heterogeneity

The increase in environmental heterogeneity improved the fitness of the subgroup with low d values. Even the number of individuals with less activated defence mechanisms exceeded the number of individuals with optimal defence levels based on

the overall environmental condition. The average d value fell to 0.857 +/- 0.183, when the environmental heterogeneity is 1.5 times as usual. A schematic diagram is shown below (Fig. 30).

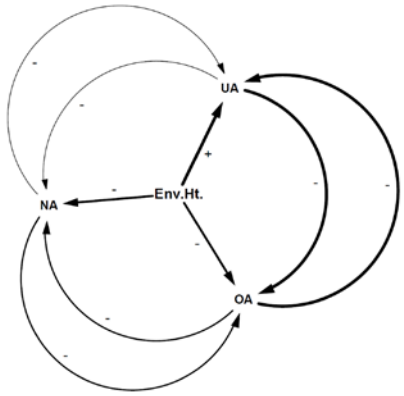

Figure 30 Effect of Environmental Heterogeneity on UA, NA and OA

The increase in environmental heterogeneity provides a broader spectrum of ecological well-being. Therefore, individuals with high mobility can gain unexpected benefit. However, individuals with high levels of defence activation are unlikely to benefit from new opportunities.

However, these results should be interpreted with caution. The simulation assumes a habitat with an average of 150 resources and one direction of resource gradient. Higher heterogeneity increases the number of patches with more than 300 resources and patches with less than 0 resources at the same time. However, the value of a patch with less than 0 resources is equal to the value of a patch with zero resources. Thus, the increase in heterogeneity only increases the number of patches favouring individuals with low defence activation levels. This is because the simulation environment assumes a single resource gradient. However, the real world consists of complex adaptive topography. In subsequent studies, it would be desirable to give

environmental heterogeneity in a variety of ways.

6. Mismatch phenomenon

When the ecological environment changes, the average *d-value* stabilises after a considerable time. Therefore, for decades of generations, individuals with suboptimal behavioural strategies for changed environmental conditions may be decreased (Di Rienzo and Hudson 2005). The temporal change of the environment may contribute to a temporary increase in the prevalence of defence activation disorder. A schematic diagram is shown below (Fig. 31).

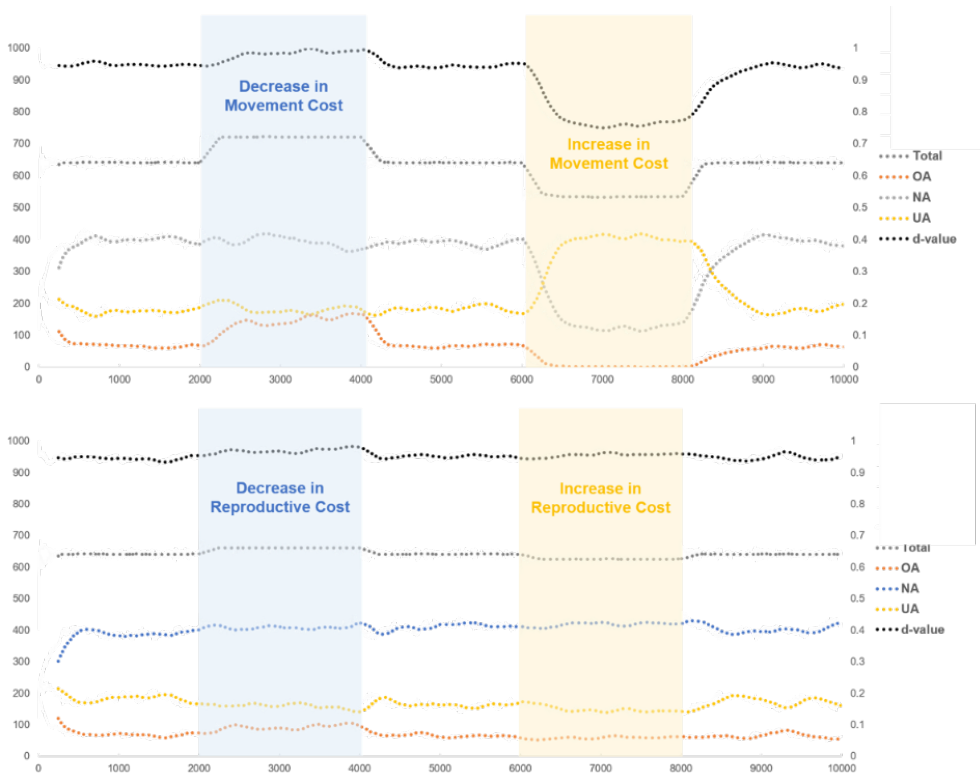

Figure 31 Schematic Diagram of Mismatch Phenomena (Movement Cost and

Reproductive Cost)

In this study, it is assumed that a simple environment in which the movement cost and the maintenance cost vary in the interval of 2 kyr over 4 times. However, the real environment changes in a more sophisticated way. In addition, the simulated environment assumes constant conditions for at least 2 kyr or 5 kyr. Subsequent studies are needed to see if the microenvironment continues to change at short intervals.

7. Limitations and Further Implications

There are some limitations to this study.

First, this simulation model does not have an evolutionary approach at the gene level. However, the full spectrum of genes related to behavioural traits is not yet clear, and genetic-level simulation studies are at a rudimentary level. It is also known that genetic competition is less likely to be the cause of the distinctive behavioural syndrome as the behavioural phenotype is under the control of the parliament of genes (Leigh 1971). Behavioural traits are complex adaptations that are dominated by many genes. Agent-based evolutionary simulations using methodological individualism (Smith and Winterhalder 1992) could be feasible way at the present level of knowledge.

Secondly, the optimal ecological model is not possible to verify why defensive behaviour is manifested in the real world (Davies 2014). However, the purpose of using the optimal simulation model is not to confirm whether individuals are behaving optimally, but to investigate qualitatively whether defensive behaviour can be explained by the criteria of optimal behaviours or constraining factors presented in the model. There may also be critical that the model and the actual defence activation phenomenon will be different. However, it is inevitable because the constraints or variables cannot, and need not, be perfect or reflect all the factors in the world (Davies 2014). The evolutionary

simulation model is handy for a qualitative approach (Frank 1998).

Third, there may be criticism that the optimal behaviour proposed in the model cannot be expressed in the real world. However, the ESS model with all the phenotypic gambit is a practical and useful research method that provides a robust approximation to a wide range of phenomena (Grafen 1984). It is especially useful in identifying the limiting factors by ABM. The purpose of this study is to confirm the maintenance of various defence activation levels in simulation environments and to estimate the constraints. The precise optimal degree of defence activation in the microenvironment or the expected prevalence of the MDD or anxiety disorder is beyond the scope of this research. Quantitative variables have only been used as a means for qualitative approaches. The ABM itself is not designed for quantitative approach. This model should not be used to estimate the amount of defence activation, that is, how often depressive or anxiety disorders occur. As demonstrated in prior research, qualitative models are superior to quantitative models in explaining ecological phenomena in general (Davies 2014).

This model shows that the fitness of the object with various *d-value* is relatively determined by the distribution gradient of the resources in the simulation habitat. It is due to the fixed environmental conditions (Davies 2014), where each agent is located, but also by the frequency-dependent mechanism of local population density (Kelly 2015). Within these conditions, there is no evolutionary significance of the so-called “the best defence activation level”, (i.e., globally ideal level mood, anxiety, fear) corresponding to the average resource value of the entire habitat. The irrational behaviour can be caused by adaptive decision process the domain of selection and the domain of testing mismatch (Houston, et al. 2007; Stevens and Stephens 2010). The optimal level of defence activation appears relative to various conditions and circumstances, and this demonstrates there is no absolute optimal value.

In general, the socioeconomic gradient of health is strongly related to depressive disorders or anxiety disorders. It is partly a direct reaction to deprivation or suffering (De

Vogli, Brunner et al. 2007), but according to this study's findings, from a long-term perspective, it may be an evolutionary outcome. Even if individuals with optimal *d-values* in the most deprived areas show suboptimal reactions to the average environment, moving to more resource-rich areas will result in higher fitness than before. Moreover, it is not included in the simplified model, but *d-value* as supraordinate appraisal guideline is likely to be adjusted through the developmental process. This model did not include any factors such as environmental plasticity, developmental plasticity, learning, communication, and cooperation. Though simplified approaches are the method of choice in evolutionary psychiatry, the results of the study should not be applied to the real world without serious consideration.

If there is no single ideal level of defence activation, the D-type disorder should be the issue of evolutionary public health rather than a focus on personal health problems (Wells, et al. 2017). The cognitive behavioural school has tried to correct the distorted schema about the ego, the world, and the future (Beck 1997). An evolutionary understanding of dysfunctional behavioural patterns may be combined with CBT (Gilbert 2002; Paul Gilbert 2004). Evolutionary analysis of mental disorders, including defence activation disorders, is not limited to an academic approach to human nature, but may serve as a scientific rationale for therapeutic intervention for sufferers.

Chapter 6. Conclusion

This study is the first agent-based simulation study about the behavioural patterns of defence activation disorder, convert it into ecological currency by using the MVT, and reconvert it to reflect the fitness in the simulation environment to find out the ultimate causations and the relationship between *d-value* and ecological constraints. In particular, the model was designed using the NetLogo programming platform, which is a robust multi-agent programmable modelling environment.

A model is an intentional representation of the real world (Starfield, et al. 1994). Real systems are often too complex to be implemented through experimentation. Therefore, a simplified representation of the system is required (Railsback 2012). Agent-based simulations are particularly useful for behavioural and evolutionary researches. Some studies are using ABM in the field of evolutionary anthropology; however, until now, ABM has never been used for the study of evolutionary medicine. Evolutionary anthropological knowledge, experience, and research methodology may expand the scope of evolutionary psychiatry.

The MVT is a well-known theorem in human behavioural ecology and a robust explanatory framework. However, except for some preliminary attempts to study mental disorders (Nesse 2019), this theorem has never been used in the field of evolutionary medicine. He refers to MVT and uses it to briefly describe the cognitive characteristics of depressive disorder, but does not mention whether it is actually applied to evolutionary psychiatric research methods. This study will confirm the value of MVT as a functional interim model for the study of neuro-anthropology.

Defence activation disorders could be results of cognitive and emotional traits that provide a pessimistic view on the self, the world and the future. Various levels of defence could be locally adaptive behaviours optimised in a variety of ecological settings. High or low level of defence activation could act as ESS in a simulated environment. They could be dysfunctional, but the outcome of an adaptive process to discourage futile

attempts and save unnecessary energy consumption. Movement cost, reproductive cost, heterogeneity of ecological environment, ecological and social mobility were identified as critical limiting factors. The fluctuation of intensity of limiting factors resulted in a temporary deterioration or improvement of the fitness of the currently optimised individuals.

There are some caveats in interpreting this study, but there are undoubtful advantages of evolutionary explanations of various dysfunctional behavioural patterns. Agent-based simulation studies on mental disorders are still in its infancy. I hope that the results of this research will be fruitful in the future. Hopefully, these challenging and courageous attempts will be fruitful in the near future.

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Supplementary Information

1 Calibration of Main Parameters

1.1 Movement Cost

Circle compares R available in the current patch (R.D.R. × R) with R of the entire habitat (M.R.D.R. × R_0). If Mov.Cost is zero; the circle will move immediately when the latter exceeds the former. If Mov.Cost is huge; the circle never moves. All circles will die soon.

What happens if the circle stays? As TSS increases, obtainable E decreases. Therefore, as the TSS increases, the circle will consider movement. UA moves first, NA moves next. OA moves most late. Suppose that Env.Ht. is 0, R_0 is 100, R.O.P. is 0.4, and R.D.R. and M.R.D.R. are 0.3. These figures are obtained by experiments of several hundred times. The expected E acquisition of the moving circle and the expected E acquisition of the staying circle are shown in Fig. 32. UA, NA, and OA are shown in orange, blue, and red, respectively (the designated colours are the same throughout the paper). The expected E acquisition of the staying circles is indicated by different kinds of black lines. When TSS is increased, the expected E for staying circles decreases

gradually.

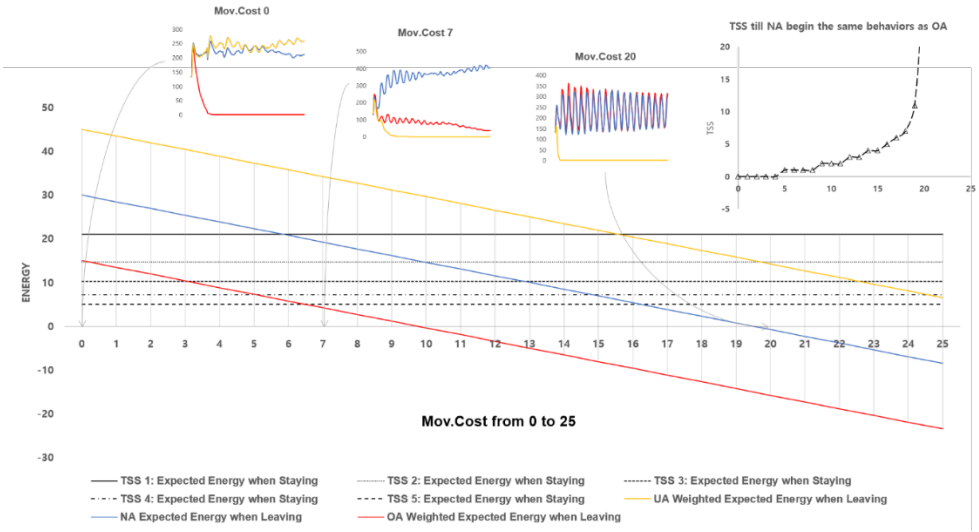


Figure 32 Weighted Expected Energy from the New Patch.

The three small graphs above show the population of each circle over time when Mov.Cost is 0, 7, and 20, respectively (Note that the circles move freely here, and the patch's R are randomly distributed). As seen in the chart, if Mov.Cost is 0, the fitness of UA and NA is the same. If Mov.Cost is 20, the fitness of NA and OA is the same.

When Mov.Cost is 7, it gets a bit complicated. When TSS is 1, the behavioural pattern of OA and NA is the same. OA and NA stay, but UA moves. If TSS is 2 or more, the behaviour of UA and NA becomes the same.NA decides to leave. If Mov.Cost is going up, UA becomes more watchful than before. If Mov.Cost is beyond 16, UA starts to stay on TSS 1. The small graph on the right above shows the TSS until NA shows the same behaviour as OA according to Mov.Cost.

As the TSS increases, (R.D.R. × R) converges to 0. However, weighted expected E of UA, NA, and OA shows a monotonic decreasing function. So, if Mov.Cost exceeds 30, 20, and 10, weighted expected E shows a negative value. Therefore, if Mov.Cost

exceeds these values, the circle will not move in any case. However, since Mnt.Cost must be considered, the TSS cannot be infinitely increased. If Mov.Cost is excessively high, all circles will die in the order of OA, NA, UA. Therefore, the value of Mov.Cost, which is appropriate for the simulation environment, should be between 4 to 20. If R.D.R. is 0.3, it should be between 6 and 20, and if it is 0.4, it should be between 10 and 20. Practically, TSS cannot be increased infinitely. If the maximum value of the TSS is regarded as about 5, it should be between 3 and 14 when R.D.R. is 0.2, and between 6 and 14 when R.D.R. is 0.2

1.2 R.D.R.

When the average R_0 is 100 and Env.Ht. is 1, the R_0 of each patch is distributed as a linear distribution between 0 and 200. If Env.Ht. is set to 25, then each R_0 is distributed as a linear distribution between 75 and 125. Under resource-poor patches, the circle should leave the patch more rapidly. Under resource-rich patches, the circle should leave the patch more slowly. Therefore, in a habitat showing environmental heterogeneity, the circles exhibit different TSS depending on the amount of each patch's resources.

R.D.R. calibration is tricky, because the expected E acquisition are differed from moving and staying circles according to the change of R.D.R.

The following assumptions were made. Mov.Cost is assumed to be 3, 7, and 12, and R_0 is 50, 100, and 150. Then, the expected E acquisition according to R.D.R. is calculated for leaving and staying. The results are shown in the following chart (Fig. 33). The red window represents the range of changes in the behaviour of OA and NA throughout 5 TSSs. The yellow window represents the range in which the behavioural tendency s of UA and NA change throughout five TSSs (Note: in some graphs the full range of red and yellow windows is not visible).

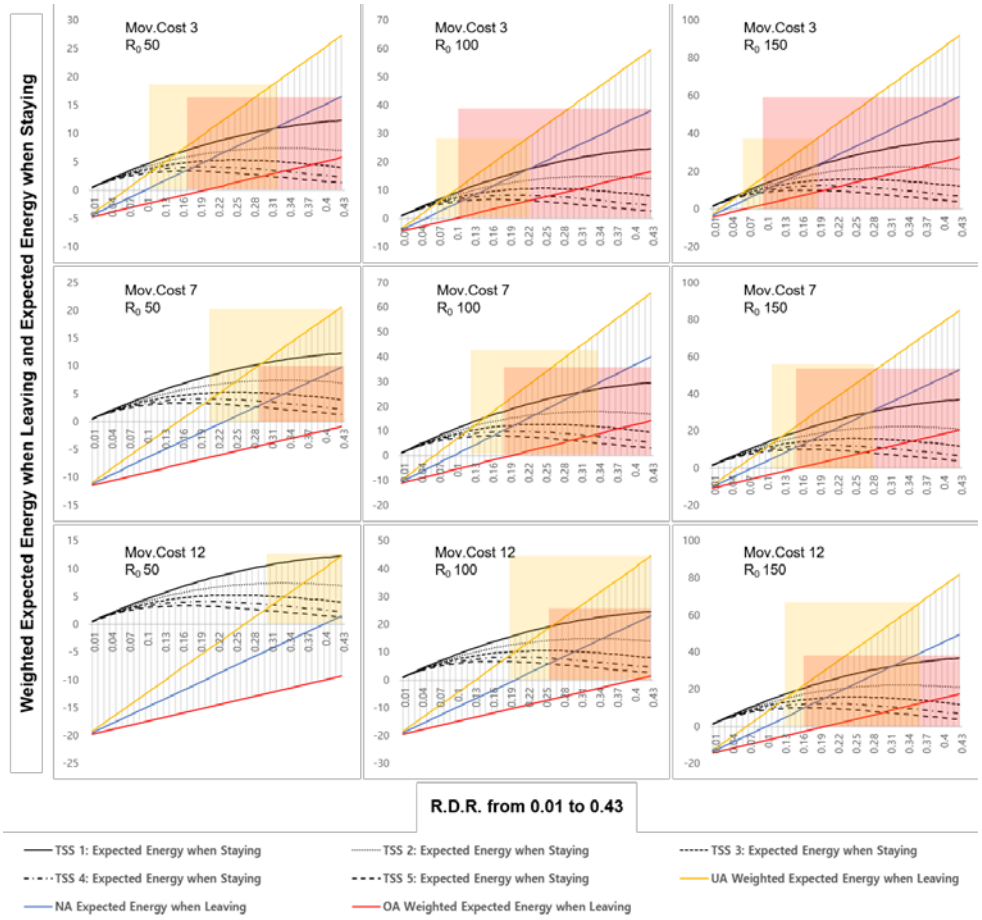


Figure 33 Weighted Expected Energy when Leaving.

Suppose TSS is a maximum of 5. If Mov.Cost is 3 and R_0 is 50 and RDR is more than 0.17, OA and NA behave differently in TSS 5. The same behaviour (staying) is seen when the RDR is less than 0.16. This pattern remains the same until the RDR is 0.65. If the RDR exceeds 0.66, OA and NA show the same behaviour (leaving). It is indicated by a red window. If the TSS diverges beyond 5 and infinitely, the lower limit is lowered until the expected E acquisition is zero, which is 0.24.

The graph shows only RDRs up to 0.43, so some segments are not shown. On the other hand, if RDR is 0.11 or more, EA and NA behave differently in TSS 5. When it

is less than 0.10, the same behaviour (staying) is shown. This tendency is the same until the RDR is 0.31. If RDR exceeds 0.32, UA and NA will show the same behaviour (leaving) again. This is indicated by a yellow window. The following table summarises the ranges of red and yellow windows for all nine cases.

Table 5 Range of Yellow Window and Red Window according to each Mov.Cost and R_0 Value

		Yellow window		Red window		
Mov.Cost	R_0	Low limit	Upper limit	Low limit*	Low limit**	Upper limit
	50	0.11	0.31	0.1	0.17	0.65
3	100	0.07	0.22	0.05	0.12	0.58
	150	0.05	0.18	0.04	0.09	0.55
	50	0.2	0.48	0.24	0.29	0.79
7	100	0.12	0.34	0.12	0.17	0.67
	150	0.09	0.27	0.08	0.15	0.62
	50	0.31	0.63	0.4	0.43	0.93
12	100	0.28	0.44	0.2	0.26	0.76
	150	0.14	0.36	0.14	0.2	0.69

* until Expected Energy when leaving go down below 0

** until TSS is 5

Taken together, if Mov.Cost is 7 and R0 is uniformly distributed between 50 and 150, the most suitable RDR should be located between 0.24 and 0.27. Since the TSS is unlikely to emerge infinitely, the largest value of 0.27 in the above range can be regarded as the most suitable RDR value. However, it is assumed that the ROP is 0.4. As the ROP increases, each window moves up. Also, as the average R increases, each window also moves down. Also, as Env.Ht. becomes higher, the width of R_0 becomes more extensive, so that the interval in which there is no proper RDR value corresponding to the R of different patches becomes longer. Overall, in an environment where Mov.Cost is 7 and

R_0 is 100, the value between 0.17 and 0.34 where the red window (assuming TSS max is 5) and the yellow window overlaps, or the value between 0.24 and 0.27 mentioned above can be considered as the suitable RDR range for stable simulation experiments.

2. Schematic Diagram of Flow Chart

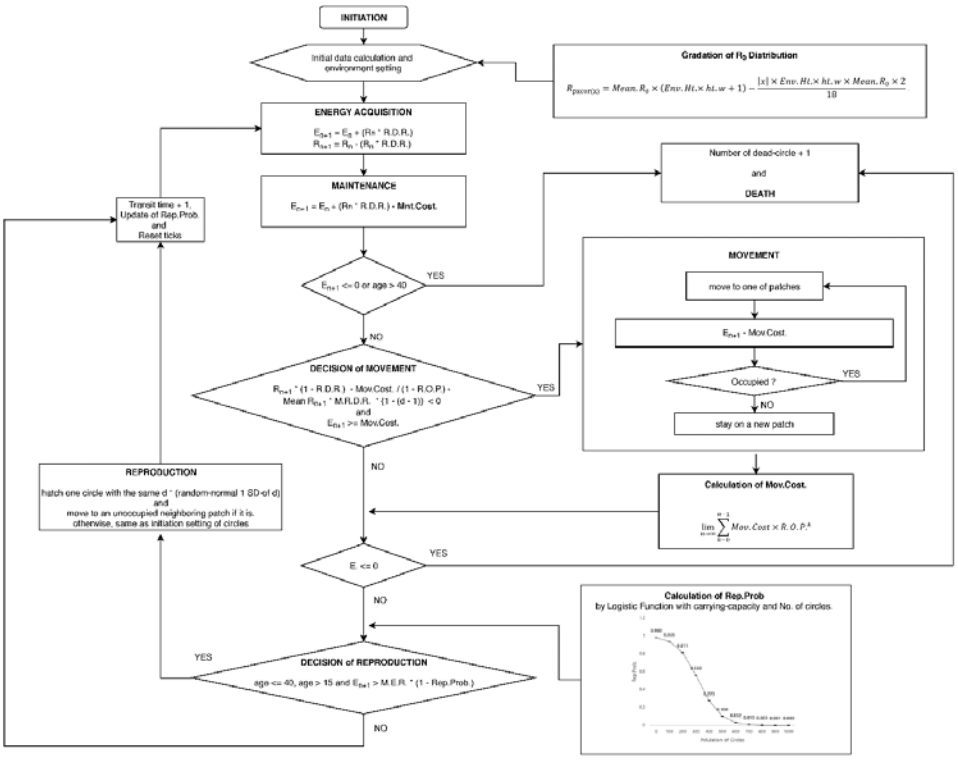
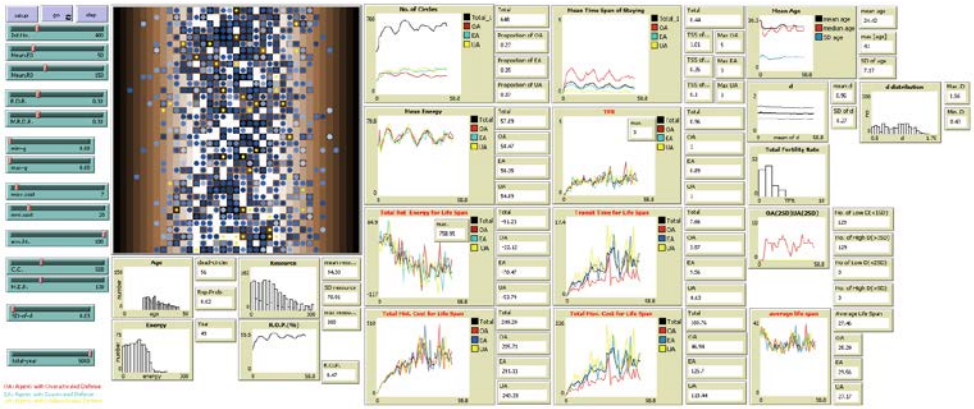
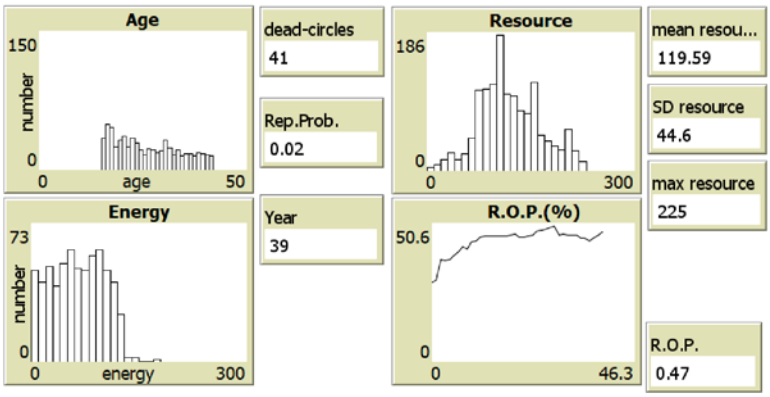


Figure 34 Flow Chart of Defence Activation Disorder Model.

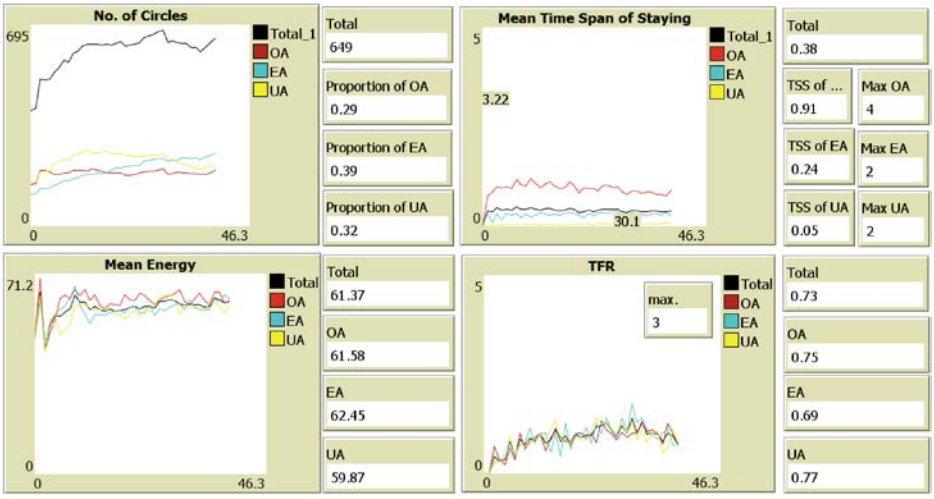
3. Display Interface of Simulation Model



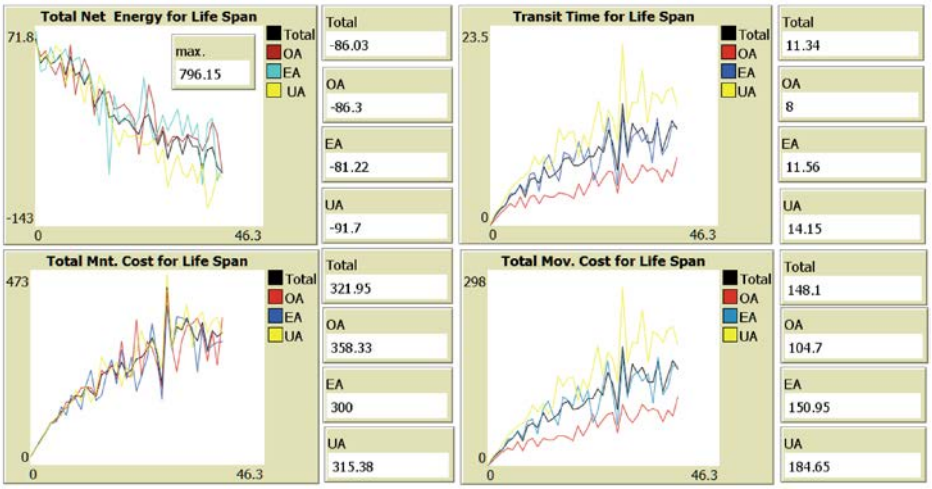
- Figure 35-1 the Entire Interface of the Simulation Model



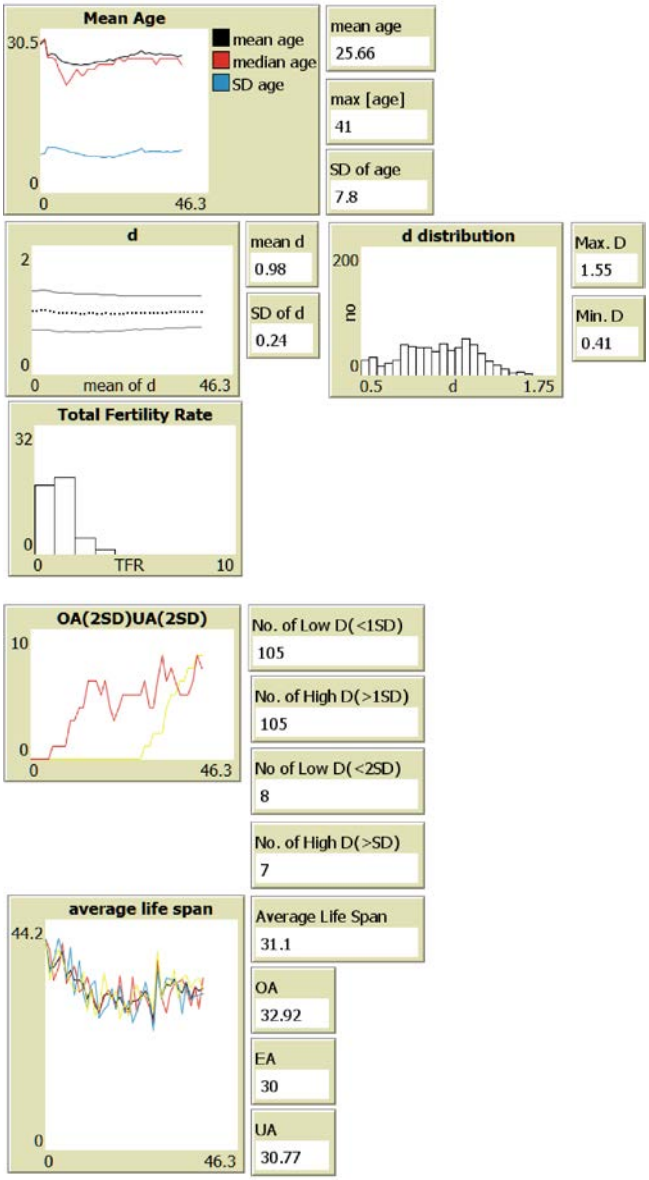
- Figure 35-2 Inspecting the Demography (Current Situation the Histogram windows of Age, Resource and Energy and the Plotting Window of R.O.P. with adjunct Monitoring Windows for Accumulated No. of Death, Rep.Prob, Year and so on)



- Figure 35-3 Inspecting the Current Situation (the Plotting Window of No. of Circles, Mean Time Span of Staying, Mean Energy and TFR with Adjunct Monitoring Windows for Inspecting the Current Situation)



- Figure 35-4 Inspecting the Accumlated Outcomes (the Plotting Window of Total Net Energy (Acquisition), Total TSS, Total Mnt.Cost, Total Mov.Cost For Lifespan with Adjunct Monitoring Windows)



- Figure 35-5 Inspecting d-value and Fitness of Agents (the Plotting Window of Mean Age, d-value, TFR, proportion of OA and UA and Life Expectancy with Adjunct Monitoring Windows)

Figure 35 Display Interfaces of Balancing Selection Model of Defence Activation

4. Code of Programme of Balancing Selection Model of Defence Activation Disorder

```
globals
[ dead-circles
  Rep.Prob.
  repro-logistic-A
  repro-logistic-B
  mov.w
  mer.w
  ht.w ]
;; global variables such as dead-circles, Rep.Prob., repro-logistic-A, repro-logistic-B, mov.w, mer.w and ht.w are declared.

breed
 [ circles
   circle ]
;; circles breed circles.

patches-own
 [ org-res
   res
   g ]
;; patches have org-rec (original resource), res (current resource) and g (regrowth rate). g is not used in the basic model.

turtles-own
 [ age
   eng
   d
   alive-or-dead
   TSS t-eng
   t-mnt.cost
   t-mov.cost
   t-tt
   t-no.ofs ]
;; circles have age, eng (energy), d (value of defence activation), TSS (time-span of staying in the current patch), t-tt (total transit time), t-eng (total energy acquired) and t-no.ofs (TFR).
```

```
to setup
 ca
  ;; clear all

  set-default-shape turtles "circle"
   ;; default shape of turtles is a circle.

   ask n-of Int.No. patches [
    sprout 1 ]
  ;; creation of circles at an initial number of patches.

  set mov.w 1
   ;; default value of mov.w is 1.
  set mer.w 1
   ;; default value of mer.w is 1.
  set ht.w 1
   ;; default value of ht.w is 1.

  ask patches

  ;; resource distribution design 1

  [ ;set org-res 300 - abs ( pxcor ) * 300 / 18
     ;;  resources  are  sequentially  graded  from  0  to  300
geographically.
    ;set org-res 250 - abs ( pxcor ) * 200 / 18
     ;;  resources  are  sequentially  graded  from  50  to  250
geographically.
    ;set org-res 200 - abs ( pxcor ) * 100 / 18
     ;;  resources  are  sequentially  graded  from  100  to  200
geographically.
    ;set org-res 150 - abs ( pxcor ) * 0 / 18
     ;; resources are equally 150 units in all patches.
    set org-res Mean.R0 * ( Env.Ht. * ht.w + 1) - abs (pxcor) *
( Env.Ht. * ht.w * mean.R0 * 2) / 18
     ;; The resources are graded sequentially according to the
ht.w value.
     ;; When ht.w is 1, the resources are scaled from 0 to 300,
and when it is 0, all the patches have the same average 150
units of resources.

    ;; resource distribution design 2

    ; [
    ;  let res1 300 - (distancexy 0 0) * 7
     ;; res1 is the value obtained by subtracting from 300 by
the value obtained by dividing 7 from distance between xycor
```

```
0.0 and the location of the patch.
    ;  let res2 150 -(distancexy 10 10) * 10
     ;; res1 is the value obtained by subtracting from 150 by
the value obtained by dividing 7 from distance between xycor
0.0 and the location of the patch.
       ;  ifelse res1  > res2
    ; [ set org-res res1 ]
    ; [ set org-res res2 ]
     ;; the resources of each patch are distributed in contour
lines  with  two  different  peaks  (300  and  150  units)  of
coordinates 0.0 and 10.10, respectively.

    ;; resource distribution design 3

   ; set org-res (mean.R0 - env.ht.) + random-float (Env.Ht. *
2)
    ;; resources are unevenly distributed according to env.ht,
but randomly distributed with no geographic orientation.


    ;; resource distribution design 4

   ; set org-res one-of [50 100 150 ]
    ;; all patches are randomly assigned one of 50, 100, or 150
units.

    ; set g min-g + random-float (max-g - min-g)
     ;; each patch is randomly assigned one g value in a linear
distribution from min-g to max-g.

     set res org-res
    ;; the initial res of the patch is set as org-res.

    set pcolor scale-color brown res 0 300
    ;; patch colour is brown, and the higher the res, the whiter
it becomes.
  ]

  ask turtles
  [ set size 0.8
     ;; circle size is 0.8
    set color blue
      ;; circle colour is blue
    set age 15 + random-float 25

    ;; d distribution design 1

    set d 0.5 + random-float 1
```

```
   ;; d-values are randomly assigned in a linear distribution
ranging from 0.5 to 1.

   ;; d distribution design 1
    ; set d one-of [ 0.66 1 1.34]
   ;; d-value is assigned to one of 0.66 1 0.34 randomly.

   ;; d distribution design 1
    ; set d random-normal 1 0.15
   ;; d-values are randomly assigned from a normal distribution
with an average of 1 and a standard deviation of 0.15.

   set eng random-float (Mean.E0 * 2 )
    ;; the circle's resources are randomly assigned in a linear
distribution from 0 to Mean.E0 * 2

   set alive-or-dead 0
    ;; initial survival or death is set to 0 (1 means death)

   set TSS 0
   set t-eng eng
   set t-mnt.cost 0
   set t-mov.cost 0
   set t-tt 0
   set t-no.ofs 0
    ;; TSS, t-eng, t-mnt, t-mov.cost, t-tt and t-no-ofs are set
as 0, but t-eng is set as initial energy.
    ]
  setup-repro-logistic

  reset-ticks
end

to go

ask turtles
 [ check-if-dead ;; check to see if the agent should die
   set age + 1 ;; to set circles to age
   recolor-turtles
   eng-acq ;; to get eng from the patch
   maintenance ;; to spend Mnt.Cost
   check-if-alive-or-dead ;; check to see if the agent should
die after spending mnt.cost
   move ;; move to another patch
   check-if-alive-or-dead-2 ;; check to see if the agent should
die after spending mnt.cost
   check-max-capacity ;; to check the max capacity
  ]
```

```
  regrow-res ;; regrow the res


ask patches
  [
    recolor-patches ;; recolor the patch according to res
  ]

   tick

  ;; to change the environment over time

  ; if ticks > 2000
  ; [set mov.w 0.5 ]

  ; if ticks > 4000
  ; [set mov.w 1]

  ; if ticks > 6000
  ; [set mov.w 2]

  ; if ticks > 8000
  ; [set mov.w 1]

  if ticks > total-year
  [stop]

  update-Rep.Prob. ;; to update the Rep.Prob.
end

to check-if-dead
  if alive-or-dead = 1 ;; check to see if agent should die
  [die]
end


to eng-acq
  set eng + res * R.D.R. ;; to get eng from the patch
  set res - res * R.D.R. ;; to reduce the amount of res from the
patch
  set t-eng + res * R.D.R. ;; to update the t-eng
end

to maintenance
  set eng - mnt.cost ;;to spend Mnt.Cost
  set t-mnt.cost + mnt.cost ;;to update the t-mnt.cost
end
```

```
to check-if-alive-or-dead ;; to update the alive-or-dead status
due to energy depletion or ageing
   if eng <= 0 or age > 40
  [set alive-or-dead 1]
end

to move
  let R.O.P. (count patches with [any? turtles-here]) / (count
patches) ; proportion of occupied patches

  if alive-or-dead = 0
  [  ifelse ( res * R.D.R. + (mov.cost * mov.w  / (1 - R.O.P.)))
< mean.R0 * M.R.D.R. * ( 1 - (d - 1))
    ;; movement design 1 : weighing mov.w, mean.R0 and 1-(d-1)

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches with [not any? turtles-here] ) * M.R.D.R. *
( 1 - (d - 1))
    ;; movement design 2 : no weighing, average res of
unoccupied patches and 1-(d-1)

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches with [any? turtles-here] ) * M.R.D.R. * ( 1 -
(d - 1))
    ;; movement design 3 : no weighing, average res of occupied
patches and 1-(d-1)

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches  ) * M.R.D.R. * ( 1 - (d - 1))
    ;; movement design 4 : no weighing,  average res of all
patches and 1-(d-1)

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) <
mean.R0 * M.R.D.R. * ( 1 / d)
    ;; movement design 5 : weighing mov.w, mean.R0 and 1 / d

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches with [not any? turtles-here] ) * M.R.D.R. *
( 1 / d)
    ;; movement design 6 : no weighing, average res of
unoccupied patches and 1 / d

   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches with [any? turtles-here] ) * M.R.D.R. * ( 1 /
d)
    ;; movement design 7 : no weighing, average res of occupied
patches and 1 / d
```

```
   ; ifelse ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches  ) * M.R.D.R. * ( 1 / d)
    ;; movement design 8 : no weighing, average res of all
patches and 1 / d

   [ if any? neighbors with [not any? turtles-here] ;; to move
to one of unoccupied neighbor
    [ move-to one-of neighbors with [not any? turtles-here]
     set eng - (mov.cost * mov.w  / (1 - R.O.P.)) ;; weighing
the mov.w with R.O.P.
     set t-tt + 1 ;; to update t-tt
     set t-mov.cost + (mov.cost * mov.w  / (1 - R.O.P.)) ;; to
update t-mov.cost
     set TSS 0 ] ;; to set TSS as 0 if move
   ]

  [set TSS + 1]] ;;to update TSS unless move

  ;; movement design 9 to 16 :apply to while loop, otherwise the
same

   ;let R.O.P. (count patches with [any? turtles-here]) / (count
patches) ; proportion of occupied patches
   ; if alive-or-dead = 0
   ; [if ( res * R.D.R. + (mov.cost  / (1 - R.O.P.))) < (mean
[res] of patches with [not any? turtles-here] ) * M.R.D.R. *
( 1 - (d - 1))
   ;    [if eng >= (mov.cost  / (1 - R.O.P.))
   ;      [ move-to one-of patches
   ;        while [any? other turtles-here]
   ;        [ move-to one-of patches
   ;          set eng - (mov.cost )
   ;          set t-tt + 1
   ;          set t-mov.cost + ( mov.cost )
   ;          set TSS 0]
   ;      ]
   ;    ]
   ;  ]
end

to  check-if-alive-or-dead-2  ;;  to  update  the  alive-or-dead
status due to energy depletion or ageing after movement
   if eng <= 0 or age > 40
  [set alive-or-dead 1]

end
```

```
to regrow-res ;; regrow res
    ask patches
  [ ifelse not any? turtles-here
    [ set res org-res ] ;; if patch is unoccupied, set res to
org-res
    [ if res < org-res  ;; unless the patch is unoccupied, set
res to res plus res multiplied by g
     [set res + res * g ]
  ]]
end

to check-max-capacity ;; to check carrying capacity
  if count patches with [not any? turtles-here] >= 1 ;; if there
is unoccupied patch, reproduce
  [reproduce]
end


to-report ratio-of-occupied-patches ;; to calculate the R.O.P.
    let R.O.P. (count patches with [any? turtles-here]) / (count
patches)
    report R.O.P.
end


to setup-repro-logistic ;; to calculate the Rep.Prob.

  let P1 0.7
  let X1 C.C. / 2
  let P2 0.1
  let X2 C.C.

  let repro-D ln (P1 / (1 - P1))
  let repro-C ln (P2 / (1 - P2))

  set repro-logistic-B (repro-D - repro-C) / (X1 - X2)
  set repro-logistic-A repro-D - (repro-logistic-B * X1)
end

to update-Rep.Prob. ;; to update the Rep.Prob.
  let total-cir count turtles
  let  logistic-Z exp (repro-logistic-A + (repro-logistic-B *
total-cir))
  set Rep.Prob. (logistic-Z / (1 + logistic-Z))
end


to reproduce
```

```
  if alive-or-dead = 0
  [if (age <= 40) and (age > 15) and eng > (M.E.R. * mer.w) *
(1 - Rep.Prob.) ;; if age and eng is enough, reproduce
    [if any? neighbors with [not any? turtles-here] ;; and if
there are unoccupied neighbor
  [set eng - ((M.E.R. * mer.w) * (1 - Rep.Prob.)) ;; to spend
reproductive cost with weighing mer.w and Rep.Prob.
   set t-no.ofs + 1 ;; to update TFR
   hatch 1 ;; set the initial setting of new circles
    [set age 15
     set size 0.5 ;; set size to 0.5 for one year
     set color yellow ;; set colour to yellow only for a while
     set d ([d] of myself)  * (random-normal 1 SD-of-d)
     set eng random-float (Mean.E0 * 2 )

    set alive-or-dead 0

    set TSS 0
    set t-eng 0
    set t-mnt.cost 0
    set t-mov.cost 0
    set t-tt 0
    set t-no.ofs 0

     move-to one-of neighbors with [not any? turtles-here] ;;
start at a new neighbor
    ]
      ]
    ]
  ]

end

to recolor-turtles ;; update the colour of circles
    set color scale-color blue age 0 50
    set size 0.8

end

to recolor-patches ;; update the colour of patches
  set pcolor scale-color brown res 0 200
end
```

5. Public Information of Programme of the Model

WHAT IS IT?

This model simulates an evolutionary model of defence activation disorder.

Populations have numerous agents with different levels of defence activation. According to Marginal Value Theorem (MVT), an agent should move to another patch in the habitat at the optimal time. For it, information on the amount of resources in the entire habitat is needed to determine the timing of movement.

However, in the natural world, it is very difficult to catch up the average amount of resource in the entire habitat. The emotion thus could act as a supraordinate cognitive module for judgement of the average amount of resources.

This model seeks to determine whether suboptimal behaviour patterns, i.e. overestimation or underestimation about the average resource amount of the entire habitat, can work as an evolutionary stabilisation strategy.

HOW IT WORKS

This model simulates an evolutionary model of defence activation disorder. The population consists of individuals with different *d-values*. Each *d-value* reflects a personal outlook on the world and future prosperity. It affects the timing of movement in the habitat through MVT.

An overly hopeful individual decides to move earlier than the average optimum. Individuals with excessively pessimistic outlooks decide to move later than the average optimum. The former represents individuals with less active defence modules, while the latter represents individuals with more active defence modules.

d-value of circles affects the movement time, which affects resource acquisition. It, in turn, affects reproductive fitness. The difference in reproductive fitness over time affects the distribution of *d-value* of the whole population.

The habitat consists of various patches with different amounts of resources, and the amount of resources is linearly distributed along the x-axis to form a gradient.

Each agent gets energy from its own patch. It costs movement costs every move and consumes maintenance costs annually. Reproduction also consumes energy for reproduction. The movement cost is relatively determined by the proportion of the occupied patches. Reproduction costs are determined by the total population, depending on the logistic function.

HOW TO USE IT

The following operations are possible.

At the initial setting, you can control population (Int.No.) and average energy levels (mean.E0), average resource level (mean.R0), and patch acquisition rate (R.D.R. or M.R.D.R.). The regeneration rate (g) of the patch's resources can also be adjusted (by min-g and max-g).

The most important sliders are movement costs (mov.cost) and maintenance costs (mnt.cost), environmental heterogeneity (env.ht.), and minimum energy requirements for reproduction (M.E.R.). It can all be adjusted with the slider. It is also possible to adjust *d-value* (SD-of-d) of the offspring, the total carrying capacity (C.C.) and the total year.

Some designs were chosen directly in the code.

I visualised the position and energy amount of each turtle (shown as circles) in the interface. Newly circles are shown in yellow. Patches are shown in brownness, with different levels of brown depending on the amount of resources.

The plot chart shows age and energy distribution among circles, resource distribution of patches, percentage of occupied resources, population, time span of staying in the current patches, time-serial patterns in average energy, total fertility rate, total energy, total number of transfers, movement cost, average lifespan, the average *d-value* and SD of d and etc.

THINGS TO NOTICE

For the model to work, the variable should not be too large or too small. Variable calibrations and the range of relevant variables are not described here. If necessary, ask by email below.

Or, see the following dissertation.

Park, H. (2019). Evolutionary Anthropological Analysis of Dysfunctional Behavioural Patterns - Focusing on Defence Activation Disorders (Doctoral dissertation). Seoul National University, Seoul, Korea.

THINGS TO TRY

Analyse the effect of various factors on the level of defence activation while controlling the movement cost, the minimum energy for reproduction, and the heterogeneity of the environment. In addition, use this model to adjust the other variables and observe the results.

EXTENDING THE MODEL

This model can be used for evolutionary analysis of various behavioural patterns. However, the appropriate sub-model of the behavioural pattern should be applied. The MVT used here may be difficult to apply to other behaviour patterns.

RELATED MODELS

If you mention this model, I ask that you include the citations below.

For the model itself:

Park, H (2019). Basic Model of Defence Activation Disorder by MVT v6.0.0. Laboratory of Evolutionary Anthropology, Department of Anthropology, Seoul National University, Seoul, Korea.

CREDITS

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국문초록

역기능적 행동 패턴의 진화인류학적 분석

– 방어활성화장애를 중심으로

인간의 신체와 마찬가지로 인간의 마음도 진화의 산물이다. 따라서 정서 체계도 긴 진화사를 통해서 빚어진 적응적 형질이다. 그런데 심리적 방어 기전은 우울이나 불안, 강박 등 다양한 정서와 관련될 뿐 아니라 위축, 복종, 자발적 패배, 회피, 무조, 보속 등 다양한 역기능적 행동과 관련된다. 방어 모듈의 과도한 활성화는 역기능적 결과를 유발하며 넓은 개념의 방어활성화장애로 분류할 수 있다. 우울장애, 불안장애, 강박장애 등의 방어활성화장애는 개체의 복리에 손해를 입힐 뿐 아니라, 직접적으로 높은 사망률과 낮은 번식률로 이어진다. 게다가 역기능적 장애는 높은 유병율과 높은 유전율을 보인다. 낮은 적합도, 높은 유병률, 높은 유전율이라는 역설적 현상을 설명하기 위해서 다양한 가설이 제시되어 왔으나 아직 만족스러운 설명은 제시하지 못하고 있다.

본 연구에서는 임계치 정리에 입각하여 정서 시스템을 환경 내 평균 자원량과 자원의 평균 감소율을 파악하는 상위 인지 모듈로 간주하였다. 이러한 가정하에서 정서 상태의 양적인 행동적 통화를 설정하고 이를 통해 개체의 적합도를 측정할 수 있는 모델을 구축하였다. 또한 본 연구에서는 전체 서식지 차원에서 최적 전략을 취하지 않는 개체가 행위자 기반 진화 시뮬레이션 환경 내에서 안정적인 비율로 유지되는 현상을 확인하였다. 개체는 자신의 방어 수준(*d-value*)에 적합한 공간적

패치에 군집하는 경향이 있었다. 개체는 국소적인 적소에 따라서 상이한 방어 수준을 가지도록 적응하였고, 상이한 방어 수준을 보이는 하위 집단의 분율은 서로 역상관관계를 보였다.

시뮬레이션 환경 내에서 최적 수준이 아닌 d-value를 보이는 하위 집단의 균형 분율이 유지되는 현상은 적소 특화 기전에 의한 것으로 보인다. 행위자는 주어진 방어 수준에 따라 국소적으로 최적화된 전략을 취하였으며, 일정한 자원 구배를 가진 이질적인 서식지 내에서 하위 집단의 상대적인 분율은 안정적으로 유지되었다. 또한 본 연구에서는 적합도에 영향을 미치는 잠재적인 생태적 요인, 즉 이동 비용, 최소 번식 비용, 환경적 이질성 등을 확인하였다. 첫째, 이동비용은 서식지 내에서 자유 이산을 제한하는 결정적 요인이었다. 이동 비용이 증가하면 전체 인구는 감소하였는데, 특히 높은 방어 수준을 가진 하위 집단의 인구가 더 많이 감소하였다. 둘째 최소 번식 비용의 증가는 인구 성장을 제한하였다. 흥미롭게도 높은 방어 수준을 보이는 개체가 번식 비용 증가에 더 취약하였다.

본 연구의 결과와 잘 부합하는 진화적 가설로서 균형 선택 현상은 최소한 행위자 기반 시뮬레이션 환경 내에서는 전체 서식지 차원에서 최적 수준이 아닌 방어 활성화 전략이 진화적 안정 전략으로 작동하도록 하는 유력한 기전으로 추정된다. 또한 이동 비용이나 번식 비용의 증가와 같은 급격한 환경 변화는 높은 방어 수준을 보이는 개체에게 부정적인 영향을 미쳤는데, 불일치 가설은 환경 변화에 직면할 때 높은 방어 활성화 수준을 보이는 개체의 역기능성이 급격히 심해지는 현상을 설명할 수 있을 것으로 보인다.

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주요어: 방어활성화장애, 진화정신의학, 정신장애, 인간 행동 생태학, 행위자 기반 시뮬레이션

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